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AT HARVARD COLLEGE.
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AN ATLANTIC "PALOLO," STAUROCEPHALUS GREGARICUS.

By Alfred Goldsborough Mayer.

With Three Plates.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
June, 1900.

No. 1. — *An Atlantic "Palolo," Staurocephalus gregarius.*

By Alfred Goldsborough Mayer.

During the summers of 1898 and 1899 I was acting as assistant to Dr. Alexander Agassiz in making a study of Medusæ at Loggerhead Key, one of the Tortugas Islands, Florida; and it was while thus engaged that the remarkable breeding habits of the worm about to be described were observed.

It gives me pleasure to express my appreciation of the generous kindness of Dr. Agassiz, to whose permission I owe the privilege of publishing this paper.

It is also a pleasure to remember the constant interest and kindness of George R. Billbury, Esq., head keeper of the lighthouse at Loggerhead Key, who did everything in his power to further the scientific work, and to render my stay at the Tortugas enjoyable.

I also wish to thank Major J. E. Sawyer, U. S. A., who kindly allowed the use of the government steamer, "George W. Childs," in transporting me and my apparatus to and fro from Key West to the Dry Tortugas.

The worm about to be described in this paper appears to possess breeding habits so closely similar to those of the well-known Palolo worm[1] of the South Pacific that I am inspired to give to it the title of the Atlantic "Palolo." Our Atlantic "Palolo," however, is a new species of the genus Staurocephalus, and is therefore quite distinct from the Palolo or Bololo worm (Palolo viridis, Gray; Lysidice viridis, Collin) of Samoa and Fiji, that swarms in vast numbers, for breeding purposes, upon the surface of the ocean, early in the morning of the days of the last quarter of the October and November moons.

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[1] It is not the purpose of this paper to discuss the habits of the Pacific Palolo. Good scientific accounts of its wonderful swarming habit may be obtained from the writings of S. J. Whitmee, 1875; W. C. McIntosh, 1885; A. Collin, 1897; B. Friedlander, 1898; and A. Agassiz, 1898. See "Bibliography" at the end of this paper.

We will first present an account of the swarming of the Atlantic Palolo, and will then give a description of the adult worm, a history of the development of its larva, and finally some general conclusions concerning the breeding habits of Polychætæ.

It seems probable that the time of the swarming of the Atlantic Palolo is directly related to the date of the last quarter of the moon, for in 1898 the swarm occurred on July 9, and the last quarter of the moon on July 10; while in 1899 the worm swarmed on July 1, and the last quarter of the moon fell on June 29. In 1898 about two hundred specimens of the worm were seen to swarm on the morning of July 8, but on the following day the animals appeared in vast numbers, while on July 10 only about a dozen specimens could be found after a careful search. In 1899 a wonderfully dense swarm appeared suddenly on the morning of July 1, and only a few worms were to be seen on July 2, after which they disappeared. As it was my habit to sail out upon the ocean early every morning, I am certain that no other swarms than the above-mentioned ones occurred between June 25 – August 19, 1898; and May 17 – July 4, 1899.

Description of the Swarming. — The swarming commenced very early in the morning before sunrise, and soon vast numbers of the worms were to be seen swimming upon the surface of the ocean. Few or none of them were to be found in the shallow water near the shore of Loggerhead Key, but at some distance to the westward of the island, where the water was between two and five fathoms in depth, they appeared in astonishing numbers. The bottom at this place is of coral-sand, and is covered with a sparse growth of Gorgonians and Nullipore Algæ, while nearer the shore the bottom consists of living coral and coral-rock with but little sand. When first observed, at four o'clock in the morning of the days of the great swarms, the worms presented very much the appearance shown in Figure 1, Plate 1. They swam with great activity and as near as possible to the surface of the sea. I estimate that there may have been about two worms to each square foot of the ocean's surface. The worms were not uniformly distributed, however, but were scattered irregularly, sometimes congregating momentarily in wriggling masses, such as were likened by Agassiz, in the case of the Fijian Palolo, to "thick vermicelli soup." These congregations are not due to any affinity for one another on the part of the worms, but are merely the result of accident, for each individual worm swims about quite independently of the others, and shows no tendency to remain in the presence of any other which it may chance to meet in its wanderings. The worms continued to increase in numbers until the time of the rising of the sun, and then, as the light of the early morning fell upon them, a series of contractions came over the sexually ripe segments of each worm and the eggs or sperm were thus discharged into the water (see Figure 2, Plate 1). This contraction is often so sudden and so violent that the ripe segments are torn asunder, at short intervals, by the breaking of the cuticula, forming large rents through which the genital products escape. The 25–30 anterior segments of the worm contain no sexual elements, and take no part in the contraction, so that they remain uninjured, and always retain their natural shape and appearance.

After the discharge of the sexual products the worms continue to swim near the surface for a considerable time, dragging their torn and contracted sexual segments after them. Sometimes, indeed, the contraction causes the sexual segments to break away from the anterior portion of the worm, and they swim about, apparently suffering no inconvenience, although without a head. After the discharge of the eggs or sperm the sexual segments become very brittle, and a touch of the hand is often sufficient to cause them to break suddenly into small fragments. It seems not improbable that the torn and contracted sexual segments may eventually slough off from the 25–30 anterior ones, and that thus the life of the individual may be saved to perpetuate the species. This, however, is mere conjecture upon my part, for in 1898 all of the worms which were confined in aquaria died during the course of the day without having thrown off their dishevelled posterior segments; and in 1899, when four of the worms were placed in a large aquarium the bottom of which was covered with sand and stones, three of the worms crawled under the stones, but all died within two days without having thrown off their contracted sexual segments.

At 6.30 A. M. the worms began to sink down upon the sandy bottom of the ocean, and by nine o'clock in the morning none of them were to be seen. Large numbers of fish devour the worms during the time of swarming.

There is little or no sexual color difference in the worms, both males and females being dull brick-red. The females, however, are sometimes of a duller and more yellowish tint than the males. The sperm is yellow-buff or slightly pink in color, while the eggs are yellow or greenish yellow. The genital products escape in such quantity that the sea is rendered milky over wide areas, and long after the worms have disappeared the eggs remain floating near the surface in visible windrows of yellowish color.

In 1900 the last quarter of the moon occurs on June 19 and July 18; and as we do not yet know the limits of the lunar month in which the worm swarms, we may look for it within three days of either of the above dates along any of the Bahama or Florida reefs. It seems not improbable that it swarms annually on one day of the year, and that this day falls within three days of the moon's last quarter in the month extending from June 15 to July 15.

Description of the Adult Worm. — The genus Staurocephalus was founded by Grube, 1855, who has given a synopsis of the genus and a description of all of the then known species in the Jahres-Bericht der Schles. Gesell. für vaterl. Cultur., Bd. 56, pp. 109–115, 1878. Since then two new species have been described by McIntosh ('**85**, pp. 231–235); and references to previously described species have been given by Ehlers, Verrill, and Andrews.

Generic Characters. — Annelida, Polychæta, Family Nereidæ; body vermiform, segments distinct. The head-lobes give rise to one or two pairs of jointed tentacles. When two pairs of tentacles are present, one pair arises from the side, and the other from the ventral surface. Eyes are sometimes present. The two first segments are without parapodia. The parapodia possess dorsal and ventral cirri. The dorsal cirrus is often unjointed, but sometimes possesses a short terminal segment. The ventral cirrus is shorter than the dorsal and is unsegmented. The posterior segment has two long dorsal and two short ventral cirri. The upper jaw consists of two simple, connected pieces. The lower jaw consists of two rod-like pieces which approach each other near the middle but diverge both in front and behind. (See Figures 20, 22, 26, 27, Plate **3**.)

Specific Characters; Adult Worm. — The worm is about 120–150 mm. in length; and may be even longer, for the posterior segment has not been observed. The segments are distinct, and there are about 17 metameres per centimetre of the worm's length. The worm is about 4 mm. broad. The ventral surface is quite flat and a deep groove runs down its centre. The dorsal surface is arched, and the dorso-ventral diameter is about 3 mm. There are no eyes, but the hypodermis cells of the front end of the præstomium bear a dark rosin-colored pigment, the presence of which may indicate a general sensibility to light. There are no lateral tentacles upon the head, but the ventral præstomium gives rise to two quite stiff tentacular cirri (see Figures 1–3, 9–12). These cirri consist each of but a single joint. An axial nerve runs down the centre of each tentacle, and this nerve is surrounded by elongate hypodermis cells. The first metamere back of the head usually bears a pair of very rudimentary parapodia, each consisting of but a short dorsal and ventral cirrus. (Figures 11, 12.) In the worm shown in Figure 3, Plate **1**, the first three segments back of the head bear very minute and undeveloped parapodia. The parapodia of the body segments are all similar each to each and consist in a well-developed dorsal cirrus, a central setigerous lobe, and a ventral cirrus that is shorter than the dorsal. (See Figure 13, Plate **2**.) The setigerous lobe bears four kinds of setæ. Most dorsal of all are three or four long curved, slender bristles having a delicately serrated edge (*a*, Figure 4, Plate **1**). Immediately below these there are three or four smaller and more slender bristles, having flat spatula-shaped distal ends that exhibit sharp serrations (*b*, Figure 4). The ventral half of the setigerous lobe bears five or six setæ of the sort shown in *d*, Figure 4; and most ventral of all there is a single thick, stiff bristle *c*, Figure 4. The blood of the worm is red, and there is a large red-colored blood sinus at the base of the dorsal cirrus of each parapodium. (See Figure 13.) The 25–30 anterior segments contain no sexual elements, these being found, however, in all of the more posterior segments. The blood vessels and nephridia of the sexually mature segments are much larger than are the corresponding organs in the anterior segments. The nephridia of the sexual segments evidently serve to carry off the eggs or sperm. The nephropores (*np*, Figure 13) are found at the base of each parapodium near the ventral surface. Sections of the worm were made, but the histology is so closely similar to that of other well-known Nereidæ that we consider it unnecessary to enter into details concerning it. The constriction of the sexual segments is due to the powerful contraction of the circular muscles that lie immediately beneath the hypodermis. The sexes are separate, and there is no distinctly marked sexual coloration. The general color of the worm is dull brick-red or ochre-red, and there is a row of diamond-shaped dull white spots, one in each metamere, running down the mid-dorsal line (see Figure 10, Plate **2**). Dark brown pigment is found around the orifice of each nephridium (*np*, Figure 13), and there are some indistinct brownish spots on the ventral side of the head (see Figure 12, Plate **2**). These are not found, however, in all individuals, and probably do not function as eye-spots.

Development. — The eggs and larvæ were killed in Perenyi's fluid, stained in Kleinenberg's hæmatoxylin, imbedded in paraffin and sectioned, the sections being usually of about 6.6 μ in thickness.

After expulsion from the body of the worm the eggs float near the surface, where they are immediately fertilized. The eggs are quite large; measurements of the embryos in the 16-cell stage gave the diameter 0.36 mm. The segmentation is total and unequal. Four large yolk-laden macromeres are cut off from the four smaller yolkless micromeres. These latter then divide repeatedly and overlap the four macromeres, and thus the gastula is formed by epibole. Although my observations are far too incomplete for anything but general conclusions, it appears that the early stages of the segmentation are strikingly similar to those of Nereis as described and figured by Wilson (**'92**).

Figure 5, Plate **1**, represents an embryo in the 16-cell stage, which occurs about three hours after extrusion into the water. It will be seen that the large macromeres are heavily laden with deutoplasm-spheres, while the protoplasm of the micromeres is finely and uniformly vacuolated, giving the appearance, when seen in sections, of a delicate network. The centrosomes are of large size and stain quite deeply in hæmatoxylin.

Figure 6 represents the condition of an embryo 9½ hours old in which the blastopore (*bp*) is just about to be closed. It will be seen that a distinct segmentation cavity (*sgc*) makes its appearance at this stage. This cavity may, however, be due to the action of reagents, and may not represent the natural condition. Unfortunately, all of my material having been killed in Perenyi's fluid, I am unable to make any statements concerning this point. It will be noticed that some of the micromeres at this stage are beginning to exhibit large intracellular vacuoles. This is especially true of those cells about 180° away from the blastopore, and also of some in the immediate vicinity of the blastopore. In later stages this vacuolization affects all of the cells of the embryo, both those of the ectoderm and entoderm, and it is certainly true that for the first week of its life the larva owes its increase in size almost entirely to the remarkable development of intracellular and intercellular vacuoles. In this connection it is interesting to note that Davenport (**'97**) has shown that in the case of tadpoles the early growth is almost entirely due to the imbibition of water. Soon after this, when the embryo is about 9½ hours old the blastopore closes, and the large deutoplasm-laden cells are completely enclosed by the micromeres. The embryos then become uniformly ciliated and swim about with considerable rapidity.

Figure 14, Plate **2**, represents an embryo 24 hours old. Two eyespots are now beginning to appear, and between these there is a collection of greenish-colored cells. These cells stain very deeply in

Kleinenberg's hæmatoxylin, and appear to be filled with a mass of deeply stained granules that may represent the coagulum of some fluid. Figures of these cells, in older larvæ, are shown in (*gl*) Figures 7, 8, Plate **1**. I believe them to be glands, and they are probably homologous with the "frontal bodies" found by Wilson ('**92**, p. 421) in the larva of Nereis, and perhaps also with the "problematic bodies" observed by Mead ('**97**, p. 256) in the larva of Amphitrite. Malaquin ('**93**, p. 395, Plate XIV., Figures 12–16) has also found glands in a similar position in the head of the larva of Autolytus Edwarsi.

Figure 15, Plate **2**, represents a larva 3½ days old, and Figure 7, Plate **1**, shows a dorso-ventral section of the same. The eyes are now quite large, and the green patch representing the gland cells is very prominent. There are now three bands of cilia: a broad oral band, a narrow post-oral, and an anal band. Two sets of setæ, consisting each of three bristles, have made their appearance immediately posterior to the post-oral band of cilia. These setæ originate in folds of the hypodermis. A longitudinal dorso-ventral section (Figure 7) of the worm in this stage shows the very large gland cells (*gl*) of the head. The mouth (*m*) shows signs of being about to break through, although as yet it is not functional. The same may perhaps be said of the anus (*an*). The mid gut (*st*) of the worm now consists of a delicate entodermal epithelium enclosing a mass of highly vacuolated cells laden with yolk spheres.

Figure 16, Plate **2**, shows a larva 5½ days old, and Figure 17 illustrates the character of the setæ from the same worm. Most dorsal of all there is a single long seta (Figure 17, *b*) and immediately below this there are two setæ of the sort shown in Figure 17, *a*.

Figure 18, Plate **3**, shows a larva 10 days old. The worm is now 0.5 mm. in length, and possesses three sets of setæ. Until the end of the 15th day the larvæ are remarkable for exhibiting a strongly positive phototaxis. They swim through the water at all depths, but large numbers of them are sure to be found clustered together in those parts of the aquaria where the light is strongest.

At the end of the 15th day the cilia disappear, and the worms cease to swim through the water, and sink to the bottom. Figures 19, 20, represent a young worm that is 16 days old, and Figure 8, Plate **1**, shows a dorso-ventral longitudinal section of the same. There are now four pairs of parapodia provided with dorsal and ventral cirri. A number of sensory hairs are found scattered over the præstomium, and the posterior segment of the body exhibits a pair of dorsal cirri.

The mouth opens on the ventral surface, and a dorsal and ventral pair of "teeth" have made their appearance in the œsophagus (see Figure 20). The worms are now about 0.8 mm. in length. Internal as well as external evidences of segmentation now appear (see Figure 8, Plate 1) and the dissepiments (*ds*) are complete. The walls of the mid gut are very thick and consist of large, irregularly shaped, highly vacuolated cells containing a number of yolk spheres. The cells of the œsophagus (*oes*) are of an epithelial character. The peripheral circular muscles and the deeper lying longitudinal muscle strands are beginning to appear, and the ventral nerve chain (*n*) is very apparent. In fact, the animal is no longer a larva, but is a young worm.

Figures 21–23, 25–27, illustrate the condition of the worm at the end of the 26th day. There are now five pairs of parapodia, and the dorsal and ventral cirri of the posterior segment have become long and prominent (see Figure 23). The dorsal and ventral jaws of the œsophagus are shown in the side view of the head given in Figure 22. Figures 26 and 27 are views from above and from the side, respectively, of the dorsal pair of jaws. The condition of the ventral pair of jaws is still quite similar to that in the 16-day-old worm shown in Figure 20. The worms are now 1.2 mm. long. They burrow readily beneath the surface of sand, but never swim through the water.

Figure 24 shows the condition of a worm 34 days old. The animal is now 1.5 mm. in length, and there are still only five pairs of parapodia. The mature coloration is beginning to appear in two reddish-colored spots immediately back of the eyes. I did not succeed in rearing any worms beyond this condition, and know nothing of the mode of formation of the præstomium and cephalic cirri of the adult worm. It will be observed that in the young worm the mouth opens on the ventral surface and the præstomium is supra-oral, while in the adult worm the præstomium and cephalic cirri are sub-oral (compare Figures 3 and 22).

General Conclusions.

Remarkably little has been written concerning the egg-laying habits of Polychætae. Wilson ('92, p. 371) states that the eggs of Nereis limbata and N. megalops are discharged at night while the animals are swimming upon the surface of the water. The egg-laying season extends at least from June until September. "The animals appear in abundance only on warm still nights, and even then are rarely found unless the water has been quiet for some days." "When the conditions are favorable, they come forth soon after dark and swim rapidly about at the surface, sometimes in almost incredible numbers."

It would probably be advantageous to any species of worm already possessed of some such egg-laying habits as those of Nereis to have the duration of the egg-laying period restricted to as short a time as possible, and also to have it occur in that part of the year most favorable for the safety and development of the larvæ. With equal numbers of mature individuals of two species (*a*) and (*b*), if (*a*) possess a long egg-laying period and (*b*) a short one, there will be more individuals of (*b*) discharging sperm or ova at any given moment than there will be of (*a*), whose breeding season is longer. Consequently the eggs of (*b*) will be more certain of fertilization, other things being equal, than those of (*a*). For example, if N represent the total number of individuals of species (*a*), and also of species (*b*); and if T represent the duration of the egg-laying period of species (*a*) and t that of species (*b*): then in any definite unit of time there will be $\frac{N}{T}$ individuals of species (*a*) discharging sperm and ova, while at the same time $\frac{N}{t}$ individuals of species (*b*) will be engaged in the same act. Consequently, if the areas of the breeding-grounds of the two species are equal, there will be $\frac{N}{t} \div \frac{N}{T}$ or $\frac{T}{t}$ times as many individuals of species (*b*) discharging sperm or ova at any moment, in a unit of area, than there are of species (*a*) engaged in the same act. Then in an area containing m individuals of species (*a*) there are $\frac{m\,T}{t}$ individuals of species (*b*). Therefore the average distance apart of the individuals of species (*a*) is $\frac{\sqrt{\frac{m\,T}{t}}-1}{\sqrt{m}-1}$ times as far as in the case of species (*b*). Hence the spermatozoæ of species (*a*) will be obliged to travel $\frac{\sqrt{\frac{m\,T}{t}}-1}{\sqrt{m}-1}$ times as far as those of species (*b*). We see, then, that a shortening of the egg-laying season causes a greater concentration of breeding individuals, and therefore shortens the average distance that the spermatozoa must travel in order to fertilize the ova; and as spermatozoa cannot survive for any great length of time, this is an advantage to the species. In this connection it is interesting to notice that according to Wilson ('92, p. 372) the males of Nereis outnumber the females to a very remarkable degree, while in Staurocephalus gregaricus, and in the Pacific Palolo, the males and females are about equal in numbers each to each. It is most essential for the perpetuation of the species that the fertilization of the ova should be insured. A very few males placed near to the females will insure this; but where the egg-laying period is a long one, and there are not often great concentrations of individuals, the males must outnumber the females in order to make certain that the ova of any given female may be fertilized.

The egg-laying period of Staurocephalus gregaricus occurred in 1898 and 1899 upon days very close to the day of the last quarter of the June-July moon. At this time, in the Tortugas, Florida, the summer is well established, the trade winds are no longer steady or boisterous, and the calm weather that precedes the hurricane season has set in. It is interesting to notice that very similar meteorological conditions prevail in Samoa and Fiji, in October and November, — the months of the swarming of the Palolo.

My friend, Dr. Charles B. Davenport, has called my attention to the fact that the advantages derived from a short egg-laying season are in some measure offset by the circumstance that under such conditions a large number of young larvæ are suddenly produced, and that therefore the struggle for food must be greatly increased. To counterbalance this difficulty, however, we have the interesting fact that while the eggs of Nereis contain but little yolk, the eggs of Staurocephalus gregaricus are heavily laden with yolk material.

When we learn more concerning the egg-laying habits of Annelids, there will no doubt be a number of species found that possess such swarming habits as those of Nereis, and perhaps a few may be discovered in which the breeding season is as short as in Staurocephalus gregaricus and Palolo viridis. In 1893, while acting as assistant to Dr. Alexander Agassiz upon the "Wild Duck" Expedition to the Bahama Islands, I had the opportunity of observing the swarming of an Annelid. We were anchored off Watlings Island (San Salvador) on the night of January 15, and in Clarence Harbor, Long Island, on the night of January 16. On both of these nights the surface of the sea was covered by thousands of little Annelids. They were translucent, and had large red eyes. They appeared to be congregating for breeding purposes, and were breaking into pieces, so that we often found fragments 50 mm. in length swimming about without a head. The last quarter of the moon occurred on January 9, 1893, and their swarming probably had no relation to this event.

Among worms, where certain segments of the body became sexually mature while others remain immature, or non-sexual, we find an interesting series of gradations in complexity. Beginning with Staurocephalus gregaricus, where the sexual and non-sexual segments are exactly alike in external appearance, and where the entire worm swims at the surface at the breeding period, the next advance in complexity is met with in Palolo viridis, where, according to Friedlander (1898) the non-sexual segments are very different in appearance from the sexual, and where the sexual segments break off from the anterior portion of the worm and swim about during the egg-laying period without a head. Most complex of all are the cases of Autolytus, Filigrana, Myriana, Proceræa, Syllis, etc. (see A. Agassiz, '62; Malaquin, '93, etc.), where the sexual segments acquire a head, and eventually become free swimming worms, thus producing an alternation of generations.

It seems probable that Staurocephalus gregaricus and Palolo viridis have independently acquired quite similar breeding habits through the agency of similar influences of natural selection; although it must still be admitted that there remains a possibility that both worms may have descended from a remote and common ancestor that possessed some such breeding habits.

The following table will serve to illustrate the principal points of relationship in the breeding habits of the two worms: —

THE ATLANTIC "PALOLO."	THE PACIFIC PALOLO.
Staurocephalus gregaricus, MAYER.	Palolo viridis, GRAY, 1847. Lysidice viridis, COLLIN, 1897.
On July 9, 1898, and July 1, 1899, the worm swarmed in vast numbers, for breeding purposes, at the Dry Tortugas Islands, Florida. The last quarter of the moon occurred on July 10, 1898, and June 29, 1899.	The worm swarms in great numbers, for breeding purposes, at Samoa and Fiji, upon the mornings of the day of, and the day preceding, the last quarter of the October and November moon. (See Whitmee, 1875; Friedlander, 1898.)
The 25–30 anterior segments of the worm contain no sexual elements, the eggs or sperm being found in the posterior body segments. The anterior segments, how-	According to Friedlander, 1898, a number of the anterior segments of the worm contain no sexual elements, these being found in the posterior body segments. The anterior seg-

ever, are similar to the sexually developed posterior ones in external appearance.	ments are of greater breadth and less length than are the sexually developed posterior segments. (See Figure by Friedlander.)
The entire worm swims at the surface during the breeding period.	The posterior or sexual segments, only, swim at the surface during the breeding period. The anterior portion of the worm remains below.
The eggs or sperm are extruded from the sexual segments by a series of contractions. They pass out into the water not only through the nephridial openings, but also through rents and tears in the body wall of the worm, which are often produced by the violence of the contractions. This action usually occurs soon after sunrise.	The eggs or sperm are extruded from the sexual segments by a series of violent contractions. They pass out into the water not only through the nephridial openings, but also through rents and tears in the body wall of the worm, produced by the violence of the contractions. This action usually occurs soon after sunrise. (See McIntosh, 1885 ; A. Agassiz, 1898.)
There is no well-marked sexual color difference, both males and females being brick-red, or ochre-red. The eggs are greenish-yellow and the sperm buff-pink.	The males are brown, and the females dark green. The eggs are green. (See Whitmee, 1875 ; McIntosh, 1885.)
The males and females are about equal in number each to each.	The males and females are about equal in number each to each.
The segmentation is total and unequal, and the gastula is formed by epibole. The larva is telotrochal. The setæ appear very early in development. The larva possesses a pair of eyes, and remarkably large ectodermal, cephalic glands.	The development is unknown.

Harvard University, April, 1899.

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PLATE 1.

Fig. 1. Staurocephalus gregaricus, nov. sp., natural size, swimming near the surface of the water before the rising of the Sun. The terminal segment has broken off, and the genital products are escaping through the orifice.

Fig. 2. Staurocephalus gregaricus, natural size, showing the worm in the act of expelling its sexual products. The eggs or sperm escape into the water through the nephridial tubules, and also through rents and tears in the cuticula of the worm. This contraction usually occurs immediately after the rising of the Sun.

Fig. 3. Side view of the head end of the worm; magnified. (*m*) mouth.

Fig. 4. Setæ of the parapodia. (*a*) are most dorsal; (*b*) next; (*d*) next; and (*c*) most ventral. See Figure 13, Plate **2**.

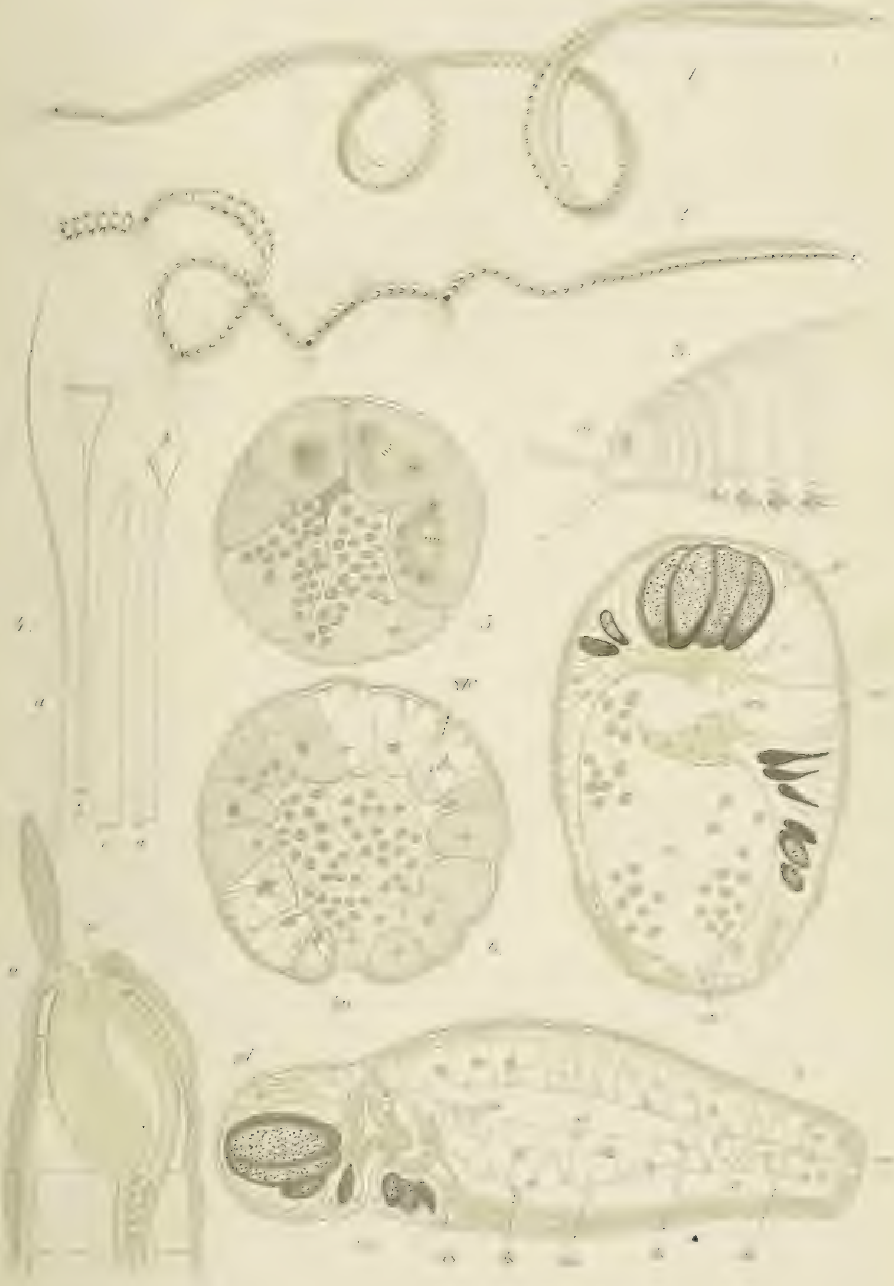
Fig. 5. Section of an embryo in the 16-cell stage, magnified 100 diameters. Age 3 hours.

Fig. 6. Section of an embryo in the gastrula stage immediately before the closure of the blastopore. (*bp*) blastopore; (*sgc*) segmentation cavity. Age 9½ hours.

Fig. 7. Longitudinal dorso-ventral section of an embryo 3½ days old, magnified 100 diameters. (*an*) place where the anus is destined to appear; (*gl*) head glands; (*m*) place where the mouth is destined to break through; (*oes*) œsophagus. (*st*) mid gut, or "stomach." The egg-membrane persists as a larval cuticula.

Fig. 8. Longitudinal dorso-ventral section of a young worm 16 days old. (*an*) anus; (*ds*, *ds*, etc.) dissepiments; (*gl*) head glands; (*m*) mouth; (*n*) ventral nerve-chain; (*oes*) œsophagus; (*st*) cavity of mid gut.

Fig. 9. Longitudinal dorso-ventral section through the head region of a mature worm, showing tentacular cirrus and muscular pharynx. The intestine of the sexually mature worm is practically empty. (*m*) mouth. (*n*) ventral nerve-chain.



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B. Meisel, lith. Boston

PLATE 2.

Fig 10. Dorsal view of Staurocephalus gregaricus, nov. sp., magnified 2 diameters. Showing the sexual segments contracted after the expulsion of the genital products.

Fig. 11. Dorsal view of head, showing mouth opening. Magnified.

Fig. 12. Ventral view of head. Magnified.

Fig. 13. Side view of parapodium of the 40th segment from the head of the worm. (*np*) nephropore.

Fig. 14. Larva one day old. Showing the green-colored gland cells between the eyes.

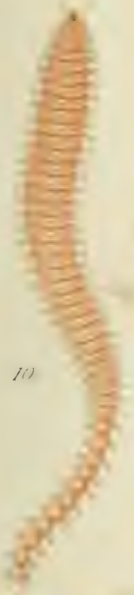
Fig. 15. Larva 3½ days old. (*gl*) head glands.

Fig. 16. Larva 5½ days old.

Figs. 17. (*a*) and (*b*) setæ of a larva 5½ days old.

MAYER-ATLANTIC "PALOLO."

PLATE 2.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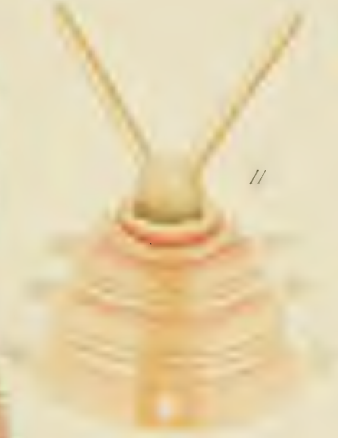
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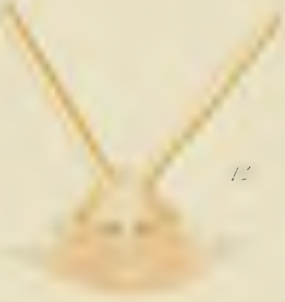
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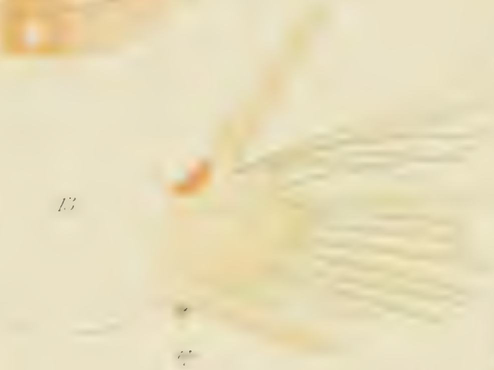
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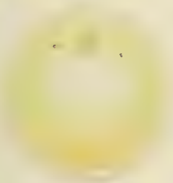
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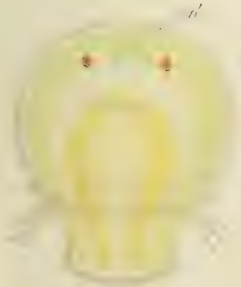
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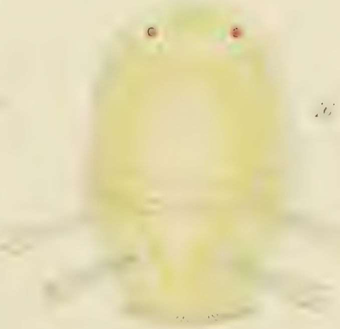
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E. Meisel lith. Boston

PLATE 3.

Fig. 18. Larva of Staurocephalus gregaricus, nov. sp., 10 days old.

Fig. 19. Dorsal view of a young worm 16 days old. The animal now ceases to swim through the water, but will readily burrow beneath the surface of sand upon the bottom of the aquarium. Length 0.8 mm.

Fig. 20. Ventral view of the head end of a young worm 16 days old, showing the "jaws" of the œsophagus.

Fig. 21. Dorsal view of a worm 26 days old. Length 1.2 mm.

Fig. 22. Side view of a worm 26 days old, showing the "jaws" in the œsophagus. (*m*) mouth.

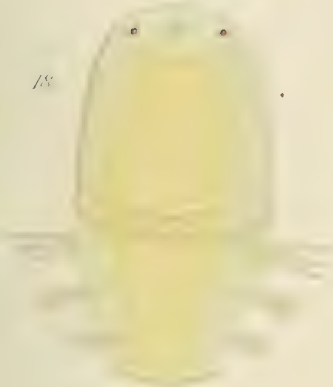
Fig. 23. Side view of the posterior segment of a worm 26 days old, showing cirri.

Fig. 24. Dorsal view of a worm 34 days old, showing the beginnings of the mature coloration immediately back of the eyes. Length 1.5 mm.

Fig. 25. Seta from a worm 26 days old.

Fig. 26. Dorsal view of the dorsal "jaws" from the œsophagus of a worm 26 days old.

Fig. 27. Side view of the dorsal "jaws" from the œsophagus of a worm 26 days old.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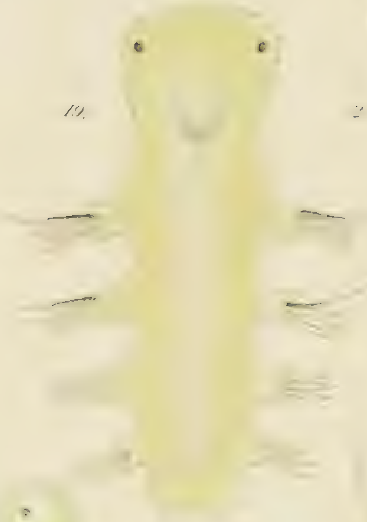
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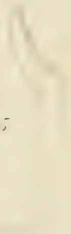
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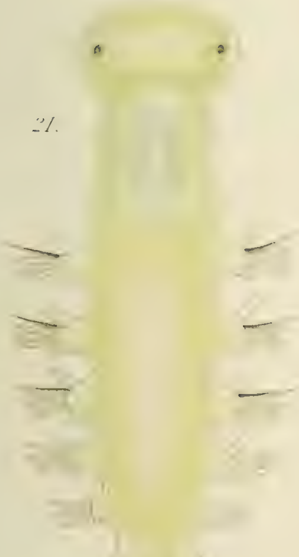
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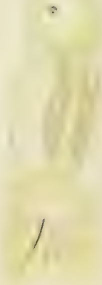
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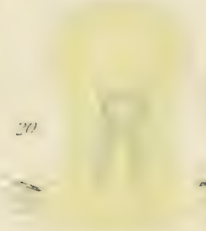
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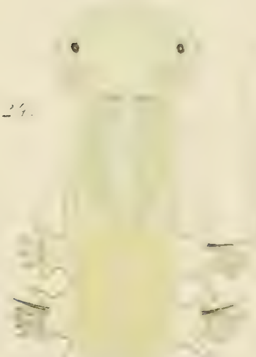
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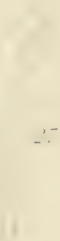
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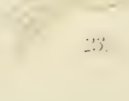
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SOME NORTH AMERICAN FRESH-WATER RHYNCHOBDELLIDÆ, AND THEIR PARASITES.

By W. E. Castle.

With Eight Plates.

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No. 2. — *Some North American Fresh-Water Rhynchobdellidæ, and their Parasites.*[1] By W. E. Castle

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. 112.

I. INTRODUCTION.

In the fall of 1897 a small leech, which is very abundant in the ponds about Cambridge, Massachusetts, was selected as an object for study in the class in Microscopical Anatomy in Harvard University. This selection brought under my observation a rather large number of leeches living or prepared in one of various ways, and gave occasion to the studies out of which this paper has grown. The kindness of friends has greatly aided me in obtaining material. In this connection my thanks are due to Mr. G. M. Allen, who sent me living leeches from the White Mountains in New Hampshire and also collected for me much valuable material in Massachusetts; to the Museum of Comparative Zoölogy for the privilege of studying its collection of leeches; to Professor James G. Needham, who sent me collections made in New York and Illinois, and also loaned me for study the collection of leeches belonging to Lake Forest University; to Dr. C. A. Kofoid, who obtained for me leeches from Havana, Illinois; to Mr. R. H. Johnson, for specimens collected in Lake Chautauqua, N.Y.; and last but not least, to Professor E. L. Mark and Dr. Otto Zur Strassen, who collected and preserved for me individuals of several European species.

Professor Whitman, who has given so much attention to the study of leeches, several years ago (**'91^a**) pointed out the inadequacy of all descriptions then existing of our North American species of "Clepsine," showing that the descriptions in question were based on characters altogether too superficial and unreliable. Whitman himself presented a model in his description of "Clepsine plana;" but as this has not been followed by any similar account of our other species, I have thought it worth while to record in this paper some observations of my own, together with the views regarding the external morphology and relationships of our common species, to which studies, chiefly anatomical, have led me.

II. METHODS.

For the study of the general anatomy of a leech and particularly for the study of its external morphology, it is important to have both living animals and those which have been killed in a good state of extension. Of the former I have been fortunate enough to obtain an abundance; in preparing the latter I have found very serviceable the method recommended by Lee ('**94**, p. 17) of stupefying with carbonated water.[1] The animals are placed in a Stender dish and covered with water from a "soda siphon." As soon as they are thoroughly stupefied, they should be quickly transferred to the killing fluid, which is best used warm, not boiling hot, but heated to about 70°C. A stay of from two to five minutes in the carbonated water usually suffices to stupefy the smaller species enough for successful fixation, and indeed is better than more prolonged treatment. For if the animal still possesses a slight degree of irritability, it will usually straighten out in the warm killing fluid and die in a better state of extension than it was in before. The large species require a much longer treatment with the carbonated water. The best reagent to use in killing animals for whole preparations is, in my experience, Perenyi's fluid, which leaves the animal well extended and renders it clear and transparent. It has the property of removing pigment from the body, particularly the darker sorts of pigment. For instance, I have noticed that in killing the beautifully variegated Glossiphonia parasitica with this fluid, the green and brown spots often disappear entirely ; while the yellow and orange spots remain conspicuous. This quality is sometimes an advantage, sometimes a disadvantage. If one wishes to preserve the color-pattern unimpaired, he would do well to use a fluid containing picric acid, which seems to have the property of fixing the pigment; or, better still, use formaldehyde both as the killing and as the preserving fluid.

Flemming's fluid is perhaps, on the whole, the best fixing fluid to use in preparing sections; corrosive sublimate is also good; Perenyi's fluid is for this purpose not to be recommended, except for the study of the gross anatomy of the central nervous system, which it makes very clear by bringing out nerves and fibre tracts in strong contrast to their connective-tissue sheaths.

Iron hæmatoxylin is the best stain which I have tried for sections. For whole preparations, animals should be heavily stained with carmine and then pretty thoroughly decolorized. I find Mayer's hydrochloric acid carmine (70% alcoholic) very convenient and serviceable, as it stains powerfully and there is no danger of maceration of tissues, however long the stain is allowed to act.

Decolorizing is best done with alcohol pretty strongly acidulated, as greater contrasts are thus obtained. I use 1% hydrochloric acid in 70%

---

[1] This method of stupefaction is also very useful in the study of the living animal, for the leech may be kept entirely motionless in the carbonated water within a live-box for hours, and then be revived by placing it again in fresh water.

alcohol, allowing it to act until the specimens have a light rose color, then wash well in neutral alcohol (90%), clear in cedar oil, and mount in balsam.

III. CLASSIFICATION.

Leeches of the family Rhynchobdellidæ may be distinguished from all others by the fact that they possess an exsertile proboscis (*pr'b.*, Figure 1), with the aid of which they obtain their food, for they are entirely without jaws such as the medicinal leech possesses. Our common North American species of this family belong to the genus Glossiphonia Johnson ('**16**), better known to many by its synonym Clepsine Savigny ('**20**). Leeches of this genus have usually a broad flat body, which, when the animal is disturbed, is rolled into a ball. Each somite consists typically of three distinct rings; but the somites at the ends of the body always contain a smaller number of rings.

These leeches are found in the shallow water of ponds and rivers underneath stones, sticks, or leaves, or adhering to the bodies of their hosts. The smaller species feed upon snails, crustacea, or other small fresh-water animals; the larger species are known to feed upon turtles, to whose shells they are often found attached. They probably suck the blood of other aquatic animals also.

The following key may aid in distinguishing the species to be described: —

Key to Species.

A. Crop diverticula a single pair (after a full meal the animal may have five more pairs, inconspicuous, and situated anterior to the principal pair); male and female genital pores separated by a single body ring; rings without metameric markings in the living animal.

1. Eyes two, distinct; a conspicuous yellowish brown chitinous spot on the neck dorsally . . . . *G. stagnalis* (p. 21)

2. Eyes two, inconspicuously pigmented or entirely without pigment; no chitinous spot on the neck; body extremely slender and transparent . . . . *G. elongata* (p. 39)

B. Crop diverticula six pairs; male and female genital pores separated by a single body ring or else united.

3. Eyes two, the middle (sensory) ring of each somite marked throughout the greater part of the body by a transverse row of whitish spots . . . . *G. fusca* (p. 34)

4. Eyes six, the first pair small and close together, the others farther apart; rings without metameric markings, or with dark pigment on the *anterior* ring of each somite.

G. heteroclita (p. 42)

C. Crop diverticula seven pairs; male and female genital pores separated by two body rings.

5. Eyes six, distinct, in two parallel rows; a conspicuous longitudinal band of dark pigment on either side of the median plane dorsally, and a fainter one ventrally; inconspicuous papillæ on the dorsal surface . . . . *G. elegans* (p. 46)

6. Eyes apparently a single pair, far forward on the head and confluent; back distinctly papillose. A large species, often found on turtles . . . . *G. parasitica* (p. 51)

IV. DESCRIPTION OF SPECIES.

1. Glossiphonia stagnalis LINNÆUS (1758).

Plate 1, Figs. 1, 3; Plate 2, Fig. 4; Plate 3, Figs. 7-10, 12; Plate 8, Fig. 34.

Hirudo stagnalis Linnæus (**1758**); H. bioculata O. F. Müller (**1774**); Clepsine bioculata Savigny (**'20**); C. modesta Verrill (**'72**); C. submodesta Nicholson (**'73**).

a. HABITAT, FORM, SIZE, COLOR.

This species is found in Europe, the adjacent parts of Asia and Africa, and in North and South America. As one might expect in the case of so cosmopolitan a form, much has been written about it, but its external morphology has never been carefully and accurately analyzed, and published accounts of its internal anatomy contain a number of errors or omissions, some of which I hope to rectify.

The general form of the body as seen in dorsal view, when partially extended, is shown in Figures 1 and 4. The body is broadest posterior to its middle and thence tapers gradually toward both ends. The head, which is only slightly wider than the neck, is evenly rounded in front (Figure 3); dorso-ventrally the body is very much flattened, especially when at rest. The animal is very active in its movements and can greatly elongate its body so as to become more than ten times as long as it is broad. The largest individuals measure as follows: —

Length, fully extended, 20–25 mm.; at rest, 8–10 mm.

Width, fully extended, about 2 mm.; at rest, about 5 mm.

Color, flesh-color or grayish. Small individuals are usually quite clear and transparent, but larger ones are apt to be more or less opaque. This opacity, as well as the general grayish tint which the body often has, is due to the presence in varying proportions of two different sorts of pigment cells. Those of one kind, which might properly be called reserve-food cells, may be found in the deeper parts of the body of all well-nourished individuals. They are large rounded cells, with an excentrically placed nucleus, their cytoplasm being filled with rounded, highly refractive granules often nearly as large as the nucleus. By reflected light these granules appear of an orange-brown color. Osmic acid browns slightly, but does not blacken them. Corrosive-acetic or picro-nitric mixtures make their composite nature apparent. An outer shell of darker, brownish substance appears surrounding usually one, sometimes two or three perfectly clear spherical inclusions. Perenyi's fluid, which is very strong in nitric acid, if allowed to act for about an hour, destroys almost every trace of the granules, the outer shell being the last part to disappear. Absolute alcohol acts in a similar way, but more slowly.

Graf (**'99**) has figured the granules accurately (see his Figures 87 and 102), but interprets their structure somewhat differently, regarding the clear portions as cavities; hence he speaks of the granules containing them as ring-shaped structures.

I at first supposed the clear portion to be a central core unaffected by the killing fluid, but abandoned this idea when I discovered two or more of them in different parts of the same granule. It seems to me that the outer part of the granule, which possibly contains some fatty material, as the osmic acid test indicates, is laid down upon a central core of a different substance which dissolves much more readily in acid solutions. So much my preparations indicate, but do not prove conclusively. Further study should be given to these interesting structures, doubtless a reserve-food product, which reminds one of the structures found in the seed of the Castor-oil Bean (Ricinus).

The second sort of pigment cell found in this species belongs to Graf's (**'99**) category of "excretophores." They occupy a superficial position in, or just under, the epidermis, and are slender, thread-like, branched (structures) of a dark-brown color. They are especially abundant in animals which have been kept for some time in well-lighted aquaria. Graf believes that pigment cells of this sort become detached as leucocytes from the wall of the body cavity, take up excretory products in the deeper parts of the body, especially in the neighborhood of the blood vessels, and then by amœboid movements make their way to the surface of the body, there to disintegrate.

b. Rings, Somites, Eyes.

External rings, rounded and distinct; sixty-seven in number, counting two narrow rings at the posterior end of the body (*64* and *66*, Figure 4, Plate **2**).

Somites, thirty-four, as in all species of Glossiphonia. Somites VI.–XXIV., triannulate (Figure 4); all other somites show more or less abbreviation.[1]

---

[1] Throughout the descriptive part of this paper I shall speak of those somites which contain fewer than three distinct rings as "abbreviated" or "reduced." I

Somites I. and II. are together represented by a single broad ring (Figures 3, 4), which, however, is sometimes subdivided by a shallow furrow (Figure 7, Plate **3**).

Somites III. and IV. consist each of a single ring, the latter forming the posterior boundary of the oral sucker (Figure 3, Plate **1**; Figure 7, Plate **3**).

Somites XXV. and XXVI. consist each of two rings, a broad followed by a narrow one (*63* and *64*, *65* and *66*, Figure 4, Plate **2**; Figure 34, Plate **8**). The narrow ring of somite XXVI., however, is often so completely fused with the broader ring which precedes it as to be scarcely distinguishable.

Somite XXVII. consists of a single broad ring, crowded back to a position lateral and posterior to the anus (*67*, Figures 4, 34, and *A*).

Somites XXVIII.–XXXIV. are not represented by external rings; in the central nervous system, however, we shall find clear evidence of their separate existence. A further discussion of the metamerism will be deferred until the nervous system has been described.

Eyes, two, large and distinct, lying in the anterior part of ring 3 and extending forward into the posterior part of ring 2 (Figures 4, 7).[1]

c. DORSAL GLAND, SUCKERS.

Dorsal Gland. — Between the twelfth and thirteenth rings (that is, between the anterior and middle rings of somite VIII.) on the mid-dorsal surface of the animal, is a structure (*gl. d.*, Figures 4, 7) peculiar to this species, though according to Apáthy ('**88**^{a}) its homologue is found in some other species, either as a functional structure in the embryo, or as an inconspicuous rudiment in the adult. It consists of a rounded, wart-like, yellowish-brown, cuticular plate, often surrounded by a ring of substance similar but lighter in color, probably because less well hardened. These structures are secreted by a patch of high columnar epidermal cells, which in the embryo, according to Apáthy, form a sort of byssus gland serving to attach the young to the under side of the mother before the suckers at the ends of the body become functional. In the adult the organ has no known function, though it forms a favorite place of attachment for a certain colonial protozoön of the genus Epistylis.

do so, however, without feeling at all certain that the terms are strictly applicable in all cases or even in a majority of cases. I have elsewhere (Castle, **1900**) expressed the opinion that the leech somite consisted primitively of a single ring. If this is so, it may well be that the somites commonly spoken of as abbreviated have really never *attained* the triannulate condition. (Moore, **1900**, has expressed a similar view since this paragraph was written.) Nevertheless the term is a convenient one to express deviation from the typical condition of the somite in the direction of a shortening of it. In this sense the term will be employed in this paper.

[1] Budge ('**49**) likewise represents the eyes in the anterior part of ring 3. Apáthy ('**88**^{a}), however, counts the ocular ring the fifth, emphasizing subdivisions which can occasionally be seen in the most anterior rings. (Compare his Figures 4 and 10 with my Figures 3 and 7.)

The *oral sucker* (*suc. or.*, Figure 7) lies on the ventral side of the head, within the limits of rings 1–3 (somites I.–IV.).

The *mouth* (*or.*, Figure 7) opens anterior to the middle of the oral sucker as well as anterior to the eyes.

The *posterior sucker* (*act.*, Figures 1, 4), also ventral in position, is slightly longer than broad. Average dimensions for the largest individuals are: — length, 1.31 mm.; width, 1.24 mm.

d. REPRODUCTIVE ORGANS.

The *male genital pore* (*po.* ♂, Figure 4) lies in a mid-ventral position between rings 24 and 25; that is, between the anterior and middle rings of somite XII.

The *female genital pore* (*po.* ♀, Figure 4), which is a broad transverse slit, lies just one ring behind the male pore, between rings 25 and 26, the middle and posterior rings of somite XII.[1]

Testes (Figure 4, *te.*), six pairs, placed intersegmentally in somites $\frac{\text{XIII.}}{\text{XIV.}}-\frac{\text{XVIII.}}{\text{XIX.}}$. The size and appearance of the testes vary considerably with the seasons. In the fall and early spring they are generally large and their outlines more or less irregular, for they adapt themselves to the spaces left them among the dorso-ventral muscles and other deep-lying organs. The testis wall is quite thick on its dorsal, ventral, and lateral aspects, but somewhat thinner on its median aspect. It is lined with a loose germinal epithelium of spindle-shaped cells, except at its dorso-median angle, where there is a small patch of ciliated epithelium continuous with that of the vas efferens.

Male genital ducts. — The vas efferens is a short, delicate tube, which leads dorsad and cephalad to join a longitudinal duct similar in structure to itself and only slightly larger, the proximal or collecting part of the vas deferens (Figure 4, *va. df.*). Anterior to the first pair of testes, that is, about on the border between somites XII. and XIII., the collecting portion of the vas deferens bends sharply toward the median plane of the body and passes between the strong dorso-ventral muscles, which, like a row of pillars, mark off on each side the lateral limits of the median lacunar space. This space the vas deferens enters in company with the ducts of the salivary glands, which here pass inward to join the base of the proboscis (Figure 1, *gl. sal.*) Having reached the median lacuna, the vas deferens turns backward, running usually ventral and lateral to the digestive tube and parallel with the course of its collecting portion. In the median lacuna it winds about more or less, or may even cross into the opposite half of the body as a result of its being crowded for room either because of its own distended condition or from the condition of other organs in its vicinity. As it runs backward it widens into a spacious seminal vesicle (Figure 4, *vs. sem.*), and its epithelial lining ceases to be ciliated. The dimensions of the seminal vesicles vary with the amount of sperm stored in them, being capable apparently of great enlargement. Sometimes the vesicle runs back as far as the pair of long crop diverticula in somite XIX. (Figure 1), and is crowded out in the form of one or more loops between the testes (Figure 4); it may even find room for itself by crossing into the opposite half of the body. Ultimately it bends forward again and, narrowing, continues as the muscular and glandular ejaculatory duct (Figure 4, *dt. ej.*). The ejaculatory duct, as it runs forward, passes outside of the inner row of dorso-ventral muscles at about the point where the collecting portion of the vas deferens enters the median lacuna. It then runs forward into somite XI., where, turning sharply back again, it expands into a thick-walled "terminal horn," which, uniting with the terminal horn of the other half of the body, opens to the outside by the mid-ventral male genital pore (*po.* ♂, Figure 4). The special function of the ejaculatory duct and particularly of its terminal horn, Whitman ('**91**) has shown to be the formation and extrusion of the spermatophore.

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[1] I am unable to find in any published account an explicit statement as to the position of the genital pores in this species. Budge (**'49**) figures the male pore in the posterior third of ring 25 and says, "Gegen den 25. Ring findet sich die sehr feine männliche Geschlechtsöffnung." He does not figure the female pore, but says (p. 100), "Ungefähr am 27. Leibesringe die äussere [female] Geschlechtsöffnung liegt." This would make the genital pores distant from each other *about* two rings, which, however, is incorrect.

Ludwig (**'86**) incorrectly describes the position of the genital pores for the entire genus "Clepsine" as follows (p. 781) "männliche Geschlechtsöffnung zwischen dem 25. und 26., weibliche zwischen dem 27. und 28. Ringel." This statement rests upon two erroneous assumptions, first, that the number of distinct rings is the same in the head region of all species, and, secondly, that the genital pores are always two rings apart. In only two of the six species described in this paper are the genital pores separated by two rings.

In the early spring, as the water in the ponds begins to grow warmer, the seminal vesicles are seen to be gorged with sperm, and the formation of spermatophores takes place rapidly. These the animals attach to one another's backs. Whitman ('**91**) has shown that in the case of G. parasitica ("Clepsine plana") the contents of the spermatophore pass through the integument into the body cavity, and that impregnation probably occurs while the egg is still in the ovary. A similar process doubtless occurs in the case of G. stagnalis.

After the period of active spermatophore formation has passed, — it ordinarily lasts but a few days or weeks, depending upon the rapidity with which the temperature of the water rises, — the vasa deferentia are seen to be greatly reduced in size and the testes quite inconspicuous, though in the fall they were the most conspicuous organ in the entire body.

The *ovaries* (Figure 4, *oa.*) are a pair of simple sacs extending back from the female genital pore in the median lacuna, usually ventral and lateral to the digestive tube. They are attached more or less loosely by mesenterial strands of connective tissue to those portions of the vasa deferentia which lie in the median lacuna. This connection, however, is so slight that when crowded for room an ovary may extend out in loops between the testes, or across into the opposite half of the body, just as the vasa deferentia do. The size of the ovaries depends upon the state of maturity of the contained ova. They are largest in the early spring immediately before the eggs are laid, when they often extend the whole length of the genital region and are looped or folded, as are the seminal vesicles; they are smallest immediately after the egg-laying. A mean between these two extreme conditions is shown in Figure 4.

The time of egg-laying, as well as of spermatophore formation, depends upon the warming of the water in the spring. One can hasten both processes by bringing the animals for a few days into a heated room. Around Cambridge the eggs are laid mostly in the months of April and May. Small-sized individuals, however, may come to maturity later in the season, even as late as September.

The eggs are pink in color and about 0.3 mm. in diameter. They are attached to the under surface of the body in groups of two to eight eggs each. Each group is enclosed in a separate, delicate, transparent sac, which adheres to the under surface of the body. The sacs are arranged in two longitudinal rows close together, one on either side of the median plane of the body. The more posteriorly placed sacs usually contain more eggs than those farther forward.

I have not observed the process of egg-laying, but believe that the eggs of a single sac are laid at about the same time, that they are then crowded back as far as possible under the body, and that there is poured over them a secretion from the clitellar glands which hardens into the delicate wall of the sac. After a period of rest, during which the body is closely applied to the group of eggs so that its sac becomes fastened to the body, another group of eggs is laid, and so on until all the mature eggs have been expelled from the ovary. The clitellar glands are deep-seated, unicellular epidermal glands opening on the ventral surface in the vicinity of the female genital pore. They can be demonstrated by methylen-blue staining.

Animals which are kept in aquaria lay their eggs at night, and always complete the process in a single night, so that all the eggs borne by an individual are in about the same stage of development at one time.

I think it probable that the egg sacs are arranged in the order laid, from behind forward, for in one of the most anterior sacs a single egg is occasionally found, but never in one of the more posterior sacs have I observed so small a number. The number of eggs laid by an individual depends upon its size. An animal thirteen mm. long (when fully extended) was found to have laid sixteen eggs; another twenty-six mm. long was found carrying forty-five eggs. The average number for nine individuals examined at one time was thirty-one.

The usual number of egg sacs formed is six or eight; in one case examined it was ten. The average number of eggs found in a sac is about four; for the most anterior pair of sacs it is three.

e. Digestive Tract.

The position of the *mouth* (*or*, Figures 3, 7), except when the body is much contracted, is anterior to the eyes, in the third somite (ring 2).

It leads dorsally into the *pharyngeal sac* (*sac. phy.*, Figure 7), which continues backward through the brain mass, ending in somite XIII. (Figure 1). Within the pharyngeal sac lies the *proboscis* (*pr'b.*, Figure 1), which, in a state of rest, usually extends from a point just behind the brain back into somite XIII., where the ducts of the *salivary glands* enter its walls. These glands (*gl. sal.*, Figure 1) are a conspicuous feature of a Glossiphonia differentially stained. They are always unicellular, and represent the largest cells found in the body except certain nephridial cells and eggs approaching maturity. The salivary gland cells have a great avidity for stains. They number in this species thirty or more in each half of the body, and are found scattered through about three somites (XII.–XIV.). The largest gland cells are those most remote from the base of the proboscis. Each cell has a separate slender duct leading into the wall of the proboscis and opening into the lumen of that organ at some point along its length.

A short slender *œsophagus* (*œ.*, Figure 1), ordinarily lying entirely within somite XIII., connects the base of the proboscis with the *crop* (*i'glv.*, Figure 1). This readily distensible part of the digestive tract extends over six somites (XIV.–XIX., Figure 1). *Under ordinary circumstances it has but a single pair of lateral diverticula;* these arise in somite XIX. and extend backward, usually ending in somite XXI. After a full meal, however, short lateral diverticula may sometimes be seen also in the five more anterior somites (XIV.–XVIII.), but this condition appears always to be a transient one.

The *stomach* (*ga.*, Figure 1) begins in somite XX. and ends in somite XXIII. It bears four pairs of persistent lateral diverticula doubtless originally segmental in origin, but now crowded within the limits of about three somites. The first two pairs of stomach diverticula are directed forward, the last pair backward; the third pair lies about at right angles to the long axis of the body.

The terminal part of the digestive tract, the *intestine* (*in.*, Figure 1), is a gradually narrowing tube; it includes one or two proximal chambers separated from the following part by constrictions.

The anus is dorsal in position, as in all other leeches, and lies within or just behind somite XXVII. (Figure *A*, page 32; Figure 34, Plate **8**). Comparison with other species, in which the reduction of somites is less extensive, shows that primitively the anus lay *behind* somite XXVII.

f. NEPHRIDIA.

The nephridia number at least sixteen pairs, possibly seventeen pairs. The nephropores (*nph'po.*, Figure 4) lie on the ventral surface of the body, somewhat nearer the margin than the median plane, and almost exactly in the middle of their respective rings. The nephropores are always found in this genus on the middle ring of a somite. I have found them in sections of G. stagnalis in somites VIII.–XXIV., with the single exception of somite XIII. (ring 28). The strong development of the salivary glands in this region may account for the possible disappearance of the pair of nephridia which we should expect to find here.

g. Nervous System.

The central nervous system, as in other leeches, consists in the middle part of the body of a ventral ganglionic chain of twenty-one distinct ganglia metamerically arranged and joined by paired connectives. Forming an extension of this ganglionic chain at either end of the body, one finds a nervous mass representing several primitively distinct ganglia more or less intimately fused together. In the central part of the body the ordinary position of the nerve ganglion is in the middle ring of its somite (Figure 4, somites XII.–XVIII.). Toward either end of the body, however, there is a slight, but increasing, centripetal displacement of the ganglia, just as is frequently the case in the central nervous system of Arthropoda. This displacement may amount to as much as two-thirds of a somite, or in extreme cases an entire somite. Thus we see in Figure 4 that the ganglion of somite VII. lies in the first ring of somite VIII., a displacement of two rings; in somites VIII.–XI. the displacement is only a single ring. About the same amount of displacement occurs in somites XIX.–XXII.; in somites XXIII. and XXIV. it amounts to about two rings; and in somites XXV.–XXVII. it is still greater. The positions in which the nerve ganglia are shown in Figure 4 are average ones carefully computed from the observed positions in five different individuals. The ganglia are very constant in position, the extreme variations usually amounting to only a fraction of the width of a ring.

The structure and morphological value of the ganglionic masses at the two ends of the body is a subject closely connected with the general question of the metamerism of the body.

h. Metamerism.

(1) *Number of Somites.*

A number of investigators have discussed the question of how many somites are found in the body of a leech, and have reached conclusions varying according as they placed emphasis on one or another of the following criteria: (1) The number of external rings; (2) color markings of rings, or the recurrence of peculiar papillæ on certain rings of each somite; (3) metameric sense organs; (4) the number of ganglia in the central nervous system as determined (*a*) by a count of the nerve capsules, typically six to a ganglion, or (*b*) by ascertaining the number and peripheral distribution of the nerves arising from the ganglia.

Whitman (**'92**), making use principally of the criteria named under 3 and 4, was the first to obtain an entirely satisfactory answer to the question. He has shown that in the central nervous system of "Clepsine hollensis" (which is closely related to G. parasitica) there are present thirty-four ganglia, each giving off paired nerves. Six of these ganglia are found in the anterior ganglionic mass which encircles the pharyngeal sac; seven are found in the posterior ganglionic mass which lies in the posterior sucker and supplies it with nerves; these, added to the twenty-one distinct ganglia found in the central part of the body, bring the total up to thirty-four. An examination of the sense organs connected with these ganglia, and situated typically on the middle ring (first, Whitman) of each somite, yields corroborative evidence that the number of somites represented in the body is thirty-four.

Bristol (**'99**) subsequently made a similar study of the metamerism of Nephelis lateralis, his conclusions being for the Gnathobdellidæ entirely in harmony with those of Whitman for the Rhynchobdellidæ.

Oka (**'94**), however, has cast doubt upon the general applicability of Whitman's determination, based as it was on the metamerism of a single species of Glossiphonia, by stating that in the several European species which he has studied (G. stagnalis, G. complanata, G. concolor, G. heteroclita, G. papillosa, G. marginata, and G. tessellata) he finds evidence of *only five* (not of six) fused ganglia in the brain. Moreover, in recent systematic papers, such as those of Blanchard (**'94**) and Moore (**'99**), we find the body of the leech still analyzed and described as consisting of twenty-six preanal somites, instead of twenty-seven, the number found in that portion of the body by Whitman (**'92**) and Bristol (**'99**), and still earlier, though on less satisfactory evidence, by Apáthy (**'88**).

Accordingly, I have thought it worth while to examine into this matter rather carefully in the case of the species studied by me.

I may say at once that my results, in the case of all six species studied, are in complete accord with those of Whitman (**'92**), so far as the *number* of metameres is concerned. In determining the *limits* of the somite, I have arrived at conclusions differing from those of my predecessors, as will presently appear (p. 31 ff.).

α. Structure of a Typical Ganglion. — A typical ganglion from the middle of the body has its ganglion cells arranged in six groups enclosed in capsules of connective tissue. Four of these capsules are lateral in position, two on each side of the ganglion; the other two occupy a mid ventral position, one in the anterior, the other in the posterior part of the ganglion. (See the ganglion of somite XXVI. in Figure 9, Plate **3**.) Three nerves are given off close together from either side of the ganglion, and are distributed to the three successive rings of one and the same somite, as I have elsewhere (Castle, **1900**) pointed out.

If, then, we can determine exactly how many such ganglia are present in the central nervous system of a leech, we shall be in a position to say how many somites enter into the composition of its body.

In the middle part of the body, as already stated, twenty-one distinct ganglia of the sort just described can easily be recognized. To determine how many are present toward either end of the body, where more or less fusion of ganglia has taken place, is a matter of more difficulty.

β. Fused Ganglia. — Figure 9 (Plate **3**) shows a dorsal view of the posterior part of the central nervous system of G. stagnalis, obtained by reconstruction from a series of frontal sections. The last two distinct ganglia, those of somites XXVI. and XXVII., are shown, followed by the nerve mass of the posterior sucker, made up of seven fused ganglia. In it seven pairs of lateral capsules appear on either side, a segmental nerve root being closely connected with each pair (XXVIII.–XXXIV.). The more posterior of the lateral capsules has in the case of each pair been displaced outward and downward (ventrad) and been reduced in size. The position of the seven pairs of ventral capsules is indicated by dotted outlines, the numeral denoting the somite to which each capsule belongs. In the first and last of the fused ganglia of this region, the ventral capsules occupy their typical tandem position (as in ganglion 26); in the case of the intervening ganglia (29–33), we find a more or less complete displacement of the ventral capsules to a side-by-side position. A similar displacement occurs in ganglion 27, which lies close back against the septum which divides the lacunar space of the posterior sucker from that in which the more anterior portions of the central nervous system lie. The same mechanical cause, crowding in an antero-posterior direction, explains both phenomena of displacement.

The evidence presented in Figure 9 leaves no room for doubt that seven primitive ganglia are found in the nerve mass of the posterior sucker in this species. Determination of the number of ganglia represented in the brain mass is not quite so easy, but the evidence is likewise convincing. The brain (*b.*, Figures 4, 7) forms a ring of nervous substance situated commonly in the last ring of somite VI. and the first two rings of somite VII. It surrounds the thin-walled pharyngeal sac (*sac. phy.*, Figure 1), there being in leeches no recognizable separation into supra- and sub-œsophageal ganglia.

A lateral view of the brain and the metameric nerves given off from it is shown in Figure 8; a view of its dorsal surface in Figure 12. Figure 10 shows the arrangement of the capsules on its ventral surface. An examination of Figures 8 and 10 shows that the capsules (*6*, *6*) of the last brain ganglion have quite their typical arrangement. A triple segmental nerve (VI., Figure 8) emerges from under a pair of lateral capsules, while below a pair of ventral capsules are arranged in the usual tandem order (*6*, *6*, Figures 8, 10).[1]

Ganglia 3–5 likewise present no special difficulties, their lateral capsules being present in pairs with nerve roots attached (*3*, *3*: *4*, *4*: *5*, *5*, Figure 8).

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[1] I have been unable to determine to what extent in the reduced somites at the two ends of the body the original triple nature of the segmental nerves persists. The nerve of the last brain ganglion is certainly triple (VI., Figure 8), as we should expect from the fact that somite VI. consists of three distinct rings (Figures 4, 7). Most of the nerves anterior to this one, perhaps all, are either double or triple, but as I have been unable to determine accurately which condition exists in some of them, I represent the nerve as undivided in the case of the first five somites (Figure 8). For a like reason I follow a similar course in representing the segmental nerves of the posterior ganglionic mass (Figure 9). I think that all of these nerves are made up of at least two distinct bundles of fibres; whether the small third nerve is also present as a distinct element in any or all of them, I am unable at present to say.

Their ventral capsules show the following modification in arrangement; they have been displaced from the typical tandem position to a side-by-side position (Figures 8, 10; compare Figure 9, somites XXIX.–XXXIII.).

The lateral capsules of ganglion No. 2 are found dorsal to the pharyngeal sac (*2*, *2*, Figures 8, 12). They seem to have been displaced backward to a position somewhat posterior to the lateral capsules of ganglion No. 3 by a migration in that direction of the supra-œsophageal commissure (Figure 8; compare Figures 11, 21). The commissure in this species is normally thrust back of the position in which it is shown in Figure 8, so that it lies about over the lateral capsules of ganglion No. 5. The animal whose brain is represented in Figure 8 was curved ventrad so that the commissure was thrust forward of its usual position and the row of lateral capsules below it was straightened out a little. The position of the ventral capsules of ganglion No. 2 is shown in Figures 8 and 10; the nerve root (II., Figure 8) arises at the anterior end of the brain just ventral to nerve root I.

The ganglionic capsules of neuromere No. 1 *all* lie dorsal to the pharyngeal sac and anterior to the supra-œsophageal commissure (Figures 8, 12). I believe that the most anterior and ventral of these (I *v*., Figures 8, 12), which lies closely attached to nerve root I. in each half of the body, is homologous with a ventral capsule of one of the succeeding ganglia. Capsule I *v*. extends out lateral to, sometimes even ventral to, nerve root I., so that its end may appear in sections between nerve roots I. and II.

Oka (**'94**) states that he finds in the brain of "Clepsine" (Glossiphonia) always *thirty* nerve capsules, and he accordingly regards it as equivalent to *five* fused ganglia and no more. Since G. stagnalis was one of the species studied by him, I am unable to understand how he can have reached such a conclusion, unless he has overlooked altogether the capsules of somite I. which lie *anterior* to the supra-œsophageal commissure.

Both the number and arrangement of the nerve capsules, and the number and position of the nerve roots, show clearly that in G. stagnalis SIX *fused ganglia are represented in the brain, and that in the entire body* THIRTY-FOUR *somites are represented.*

(2) *Somite Limits.*

It remains to explain the grounds on which the limits of the somites have been placed by me as indicated in Figure 4. Whitman (**'85**) pointed out many years ago that a certain ring (the first, according to his account) of each typical somite in the body of a leech is more richly supplied with sensory organs ("sensillæ") than any other ring of the somite. In many species of Glossiphonia special color markings or papillæ are also found on the sensory ring. Color markings, however, are wanting in G. stagnalis, and the sensillæ are not sufficiently conspicuous in the living animal to make identification of the sensory rings at all certain. But a carmine stain of the proper intensity renders identification of the sensory rings quite easy by giving them, especially along the margins of the body, a somewhat darker color. Observing this fact, I was first enabled to determine as sensory the rings indicated by Arabic numerals in the right half of Figure 4; further study revealed the presence of marginal sensillæ in the positions indicated in Figure 3.

The metamerically repeated sensory annuli were thus positively identified throughout the greater part of the body. It remained merely to mark off the somite limits between successive sensory annuli. This I at first did after the usage of Whitman (**'85, '92**) and practically all others since the time of Gratiolet (**'62**), considering the sensory ring as occurring *at the anterior end of its somite.*

I found, however, that a consistent following of this practice would, toward either end of the body, place the somite limits *in the middle of a ring* instead of between rings, the position in which somite boundaries fall in other regions of the body. See Figure *A*, XXV'., XXVI'., etc.

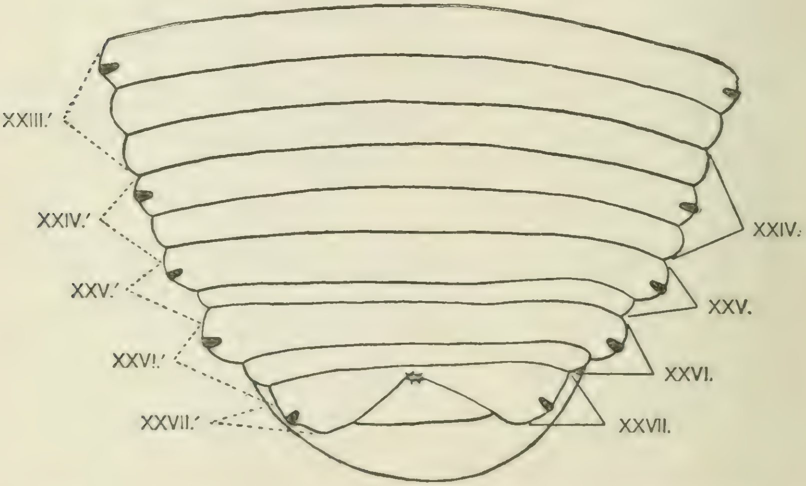

FIGURE *A*. — *G. stagnalis.* Dorsal view of posterior part of body, showing marginal sensillæ. Somite limits are indicated correctly at the right of the figure (XXIV. to XXVII.); at the left of the figure (XXIII'. to XXVII'.) they are shown as they have been commonly but incorrectly placed.

This led me to inquire whether the sensory ring really is the anterior ring of its somite. The results of this inquiry have been published elsewhere (Castle, **1900**), so that only one or two of the more important conclusions need be restated here. One of these, already suggested in part on page 29, is the following: —

Somite limits coincide with neuromeric limits; consequently in Glossiphonia the sensory ring is the middle, not the anterior ring of the somite.

This point being established, the somite limits must be marked off, in the regions where unabbreviated somites occur, as in Figure 4, VI.–XXIV.

I have further shown, in the publication already cited, that in Glossiphonia somite abbreviation[1] is accomplished by a series of steps which follow one another in regular sequence. First, a union takes place between the sensory ring and the ring which precedes it; secondly, the ring which follows the sensory ring is reduced in size; finally, it too fuses with the sensory ring, the entire somite being then represented by a single external ring.

If, as is not improbable, some of the "abbreviated" somites are really in arrested stages of development from the one-ringed to the three-ringed condition (as suggested in the case of Microbdella by Moore, **1900**), the order of the three steps enumerated should be reversed, in their case, and described in the following terms: (1) A distinct narrow ring is separated off at the posterior end of the uniannulate somite; (2) this newly formed posterior ring grows in width; (3) another new ring is separated off at the *anterior* end of the somite. This produces a three-ringed somite, all three rings ultimately attaining an equal width. For convenience in description, however, the process will be uniformly treated as one of abbreviation, as explained on page 22, footnote.

The amount of "abbreviation," as is well known, becomes greater toward either end of the body.

Bearing in mind these principles, we find that the least affected of the abbreviated somites of G. stagnalis are those which stand nearest to the unabbreviated somites, namely, V. (Figure 3) at the anterior end of the body, and XXV. (Figure *A*) at the posterior end. In the case of each of these, the anterior and sensory rings of the somite are united into a single broad ring. But in the case of somite V. we find the union occasionally incomplete, as indicated by the notch (less clearly than it should be) at the upper margin of Figure 3, ring 4.

Somite XXVI. (Figure *A*; Figure 34, Plate **8**) is usually found in the same condition of abbreviation as the somites just described. Occasionally, however, its posterior ring is narrower or less distinct than that of somite XXV.

In somites III. and IV. the process of abbreviation to a single broad ring is practically complete, although the narrow posterior ring is in favorable preparations still recognizable as a distinct element separated from the rest of the somite by a shallow transverse furrow (Figure 7, III., IV.).

Somites I., II., and XXVII. have each been reduced to a single ring; in addition a fusion (sometimes incomplete) has taken place between somites I. and II., so that they are together represented by the broad ring, 1 (Figure 7).

Somites XXVIII.–XXXIV. are not represented by annuli on the surface of the body; they form collectively the posterior sucker.

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[1] As to the sense in which this term is used, see p. 22, footnote.

2. Glossiphonia fusca sp. nov.

Plate 4.

a. HABITAT, FORM, SIZE, COLOR.

This species is rather closely related structurally to G. stagnalis, with which I have found it associated in the vicinity of Cambridge, Mass., and Trenton, New Jersey. It is of about the same size as G. stagnalis, but is broader in proportion to its length (Figure 13, Plate **4**). In its movements it is somewhat more sluggish than that species and does not stretch itself to so great a length.

Length of largest individuals, fully extended, 20 mm.; at rest, 9 mm.

Greatest width, when fully extended, 2.5 mm.; at rest, 4 mm.

Color, a coffee-brown above, somewhat lighter below. The general brown coloration is due to the presence in the superficial layers of the body of slender, branched, thread-like pigment cells bearing numerous knot-like swellings and filled with a dark-brown pigment. Such pigment cells are clearly homologous with the pigment cells found in a superficial position in the body of G. stagnalis, — Graf's "excretophores." They are much more abundant on the dorsal than on the ventral surface. On the former they appear in greatest numbers in a median dark band about as wide as two or three body rings; but they are entirely wanting anterior to the eyes and in the following regions, which therefore appear as clear, transparent areas: —

1. A transverse row of circular spots found on the sensory ring of each somite. These spots are about the width of a ring in diameter. Their maximum number is seven, but it is a rare occurrence to find all seven present in a single somite. Each spot occupies a definite position on its ring, so that those of successive somites form seven longitudinal rows, three in each half of the body and one median in position. The paired rows may be designated as *marginal*, *intermediate*, and *paramedian*, for they occupy positions which correspond closely with those of the rows of dorsal papillæ so designated in the case of G. parasitica (Plate **2**, Figure 6).

The paramedian rows of clear spots are more constant in occurrence than any of the others; they can usually be found on somites v.–xxvi. The intermediate and marginal rows usually begin about in the region of the genital pores and continue with increasing distinctness back to the anus. The median row is less well developed than any of the others. It is represented by an occasional clear spot in the region posterior to the genital pores and anterior to somite xxii.

2. In the region of somites xxii.–xxvi., the median row of clear spots is suddenly replaced by a continuous clear band about as wide as one of the spots. Along the margins of this clear band, the pigment is unusually abundant, which fact adds by contrast to the conspicuousness of the median band.

3. The margin of the posterior sucker, where it projects beyond the outline of the body as seen in dorsal view, usually bears eight or ten triangular or

rounded clear spots of approximately the same form and position as the yellow pigment spots found on the posterior sucker of G. parasitica (see stippling in Figure 6).

4. The sensory ring of each of the somites in the neck region — somite v. and a few of the following — is occasionally distinguished by an uninterrupted, but narrow, clear band, which runs entirely across it from one side of the body to the other, occupying about its middle third.

The conspicuousness of the unpigmented areas just described, except that mentioned under (4), is increased by the presence in the centre of each of a group of peculiar reserve-food cells, which lie quite near the surface of the body.

The *ordinary reserve-food cells* of this species agree in practically every particular of structure and distribution with those of G. stagnalis. They are large rounded cells, sometimes attaining a diameter of eighty mikra or more. The granules within their cytoplasm attain a diameter of six or seven mikra. The color of these cells by reflected light is a pale orange; by transmitted light, they are semi-transparent, of a leaden gray color. They are distributed irregularly through the middle and posterior portions of the body, being situated in its deeper parts.

The *special form of reserve-food cell*, which is found in the segmental clear spots already described, differs in respect both to size and to color from the ordinary reserve-food cell. It is considerably smaller, — forty to fifty mikra being the maximum diameter observed, — and its contained granules are likewise smaller, though more numerous. Its color by reflected light is a bright lemon yellow; by transmitted light it is brown. Finally this variety of reserve-food cell is invariably situated quite near the surface of the body. The appearance of a group of these cells as seen under a moderately high power of the microscope is shown imperfectly in Figure 17 (Plate **4**).

The ventral surface of the body is pigmented in very much the same fashion as the dorsal, but less heavily. There is, however, this difference in the distribution of the superficial brown pigment: on the ventral surface a pair of narrow, paramedian, pigmented lines can be recognized, one in each half of the body, in about the position of those found both dorsally and ventrally in G. elegans (Figure 30, Plate **7**). On the dorsal surface, on the other hand, the most heavily pigmented region is a broad median band (p. 34).

Segmental clear spots are found on the sensory rings on the ventral surface also, and these are arranged in paramedian, intermediate, or marginal rows; but the spots are much less conspicuous than on the dorsal surface, and the lemon-yellow reserve-food cells are less often found in their centres.

Comparing the coloration of this species with that of G. stagnalis, we may say that the histological elements which produce the coloration are very similar in the two, but the distribution of these elements is such as to produce in G. fusca a distinct color pattern (longitudinal striations and segmental clear spots), a feature entirely wanting in G. stagnalis.

b. Rings, Somites, Eyes, Suckers.

External rings, not quite so distinct as in G. stagnalis ; skin, slightly rougher owing to the stronger development of Bayer's (**'96**) sense organs. Number of preanal rings, seventy (Figure 13, Plate **4**).

Somites V.–XXIV. are triannulate, but the two anterior rings of V. are united ventrally (Figure 15).

Somites I. and II. are included in a single broad ring, which, just as in G. stagnalis, is sometimes subdivided by a shallow transverse furrow (Figure 14) marking the boundary between the two incompletely fused somites.

Somites III., IV., XXV. and XXVI. (Figures 13–16) are biannulate. In each case the broader, anterior ring bears the sensillæ and corresponds to rings 1 and 2 of triannulate somites (compare somites IV. and V. of Figure 15).

Somite XXVII. is a single broad ring (70, Figure 13) which lies just anterior to the anus, not crowded back of it, as in stagnalis (Figure 34, Plate **8**).

The principal differences in somite composition between fusca and stagnalis occur in the head region, in somites III.–V. These somites are less abbreviated (or more fully elaborated) in fusca than in stagnalis, hence the greater number of preanal rings in the former (seventy) as compared with the latter (sixty-seven).

Eyes, two, large and distinct, situated in rings 3 and 4 (Figures 14–16). The sensory elements of each eye, as in G. stagnalis, are contained in a pigment cup which is open only on its anterior, lateral surface, where the nerve fibres make their exit (Figures 14, 16).

Oral sucker, as in all species of Glossiphonia, included within the first four somites (Figures 14, 15).

Posterior sucker of about the same dimensions as in G. stagnalis, slightly longer than broad.

c. Reproductive Organs.

Male genital pore (*po.* ♂, Figure 13), between the first and second rings of somite XII. (rings 27 and 28).

Female genital pore (*po.* ♀, Figure 13), between the second and third rings of somite XII. (rings 28 and 29).

Testes (*te.*, Figure 13), six pairs situated intersegmentally in somites $\frac{\text{XIII.}}{\text{XIV.}}-\frac{\text{XVIII.}}{\text{XIX.}}$

The *ovaries* have the usual form and position of these structures in other species, being found ventrally in the median lacuna.

Eggs are laid a month or six weeks later than by G. stagnalis (June 12, 1898, Cambridge, Mass.). In color they resemble those of G. stagnalis closely, being of a light pink or flesh color. As in G. stagnalis, the eggs are attached to the under side of the body posterior to the genital pores, within a number of delicate sacs arranged in two parallel rows, close together, one on each side of the median plane. The number of sacs is most often six, but a seventh sac was observed in one case. The number of eggs in a sac, as well as the total number of eggs laid by an individual, is greater in this species than in G. stagnalis. The following figures will indicate the number of eggs borne by four good-sized individuals, which laid eggs in the laboratory in June, 1898. The vertical line represents the median plane of the body; the positions of the numerals show how the sacs were placed with reference to one another and to the median plane of the body; the numerals themselves indicate how many eggs were in each sac. Anterior is toward the top of the page, and the right side of the body toward the left of the page, the animals having been observed in ventral view.

INDIVIDUAL I.

a.

	16	17	
r.	16	20	*l.*
	22	13	

p.

Total 54 + 50 = 104

INDIVIDUAL II.

a.

	11	6	
r.	15	13	*l.*
	18	14	

p.

44 + 33 = 77

INDIVIDUAL III.

a.

	2	13	
r.	18	20	*l.*
	19	18	

p.

39 + 51 = 90

INDIVIDUAL IV.

a.

		5	
	16	14	
r.	21	19	*l.*
	17	13	

p.

54 + 51 = 105

Average number of eggs in a sac in above cases, 15 (as against 4 in G. stagnalis); average number of eggs borne by an individual, 94 (as against about 30 in the case of G. stagnalis).

It will be noticed that one of the anterior sacs often contains a relatively small number of eggs (as noticed in the case of G. stagnalis also), suggesting that it served to finish off the egg-laying, the sacs being arranged in the order in which they were formed, from behind forward.

d. DIGESTIVE TRACT.

The *mouth* is situated anterior to the eyes, well forward in the anterior half of the oral sucker (Figures 14, 15). From here the thin-walled *pharyngeal sac* (*sac. phy.*, Figure 13) leads back to the base of the proboscis in somite XII., just behind the male genital pore. When the animal is at rest the *proboscis* (*pr'b.*, Figure 13) usually extends through the four somites between the brain and the male genital pore (VIII.–XI.) into somite XII., where it receives the ducts of the salivary glands, a bundle from either side of the body.

The *salivary glands* themselves are very large in this species and are distributed in the marginal part of the body through somites XI.–XVII., or, in exceptional cases, even a somite farther in one direction or the other.[1]

The short *œsophagus* (*œ.*, Figure 13) extends from the base of the proboscis through somite XIII. to the beginning of the crop in somite XIV.

The *crop* (*i'glv.*, Figure 13) extends over the six somites XIV.–XIX., giving off in the middle of each a pair of conspicuous lateral diverticula. *These are always evident whether the crop contains food or not*, a condition very different from that which exists in G. stagnalis. The last pair of crop diverticula (those of somite XIX.) are very long but simple, as in G. stagnalis, without secondary lateral diverticula. They extend back over the entire stomach region, usually ending in somite XXIII.

The *stomach* (*ga.*, Figure 13), which is separated from the crop by a valve-like constriction, bears four pairs of lateral diverticula doubtless originally metameric in arrangement, but now arising within the limits of somites XX.–XXII.

The *intestine* (*in.*, Figure 13) leads from the stomach back to the anus, which is situated dorsally just behind somite XXVII., as in other species of Glossiphonia. The intestine includes anteriorly two rather spacious chambers, the first of which bears a pair of small ear-like diverticula from its anterior lateral borders. Behind these chambers comes a simple tubular part terminating at the anus.

To sum up, *the particulars in which the digestive tract of G. fusca differs conspicuously from that of G. stagnalis are* (1) the shorter proboscis and larger œsophagus; (2) the larger salivary glands, distributed through a greater number of somites; (3) the persistent character of the first five pairs of crop diverticula; (4) the distinctly chambered condition of the intestine, and the pair of diverticula borne by its first chamber.

Nephropores are found on the sensory ring of each of the somites VIII.–XXIV., with the possible exception of XIII., where, as in stagnalis, the nephridia are much reduced, if not wholly wanting, — a fact accounted for by the strong development of the salivary glands and genital ducts in that region. The nephropore lies usually a little anterior to the middle of the ring on which it is found.

c. NERVOUS SYSTEM.

A ventral view of the brain is shown in Figure 18, a dorsal view of that part of it which lies above the pharyngeal sac is shown in Figure 16, the position of the ventral part being indicated by a dotted line; the outline of the brain as seen in a lateral view is shown in Figure 14, *cb.* It lies for the most part in somites VII. and VIII. This is about a somite posterior to the usual position of the brain in G. stagnalis (Figures 4, 7).

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[1] The animal shown in Figure 13 was a small one, and the salivary-gland cells are proportionally a little larger than they would be in the average, full-grown animal.

The number of fused ganglia represented in the brain is, as in G. stagnalis, six, and the nerve capsules have the same general arrangement as in that species. The ventral capsules of neuromeres II.–V. are placed side by side, while those of neuromere VI. lie one behind the other (Figure 18; compare Figure 10, Plate **3**). The six capsules of neuromere I. are situated well dorsal, as in G. stagnalis, and the supra-œsophageal connective is pushed back nearly over the middle of the entire brain mass (Figures 14, 16). The lateral capsules of neuromere II. are shown in the dorsal view (Figure 16); those of neuromeres III.–VI., in the ventral view (Figure 18).

In Figure 14, which represents a parasagittal section, is shown the position of the paramedian sensillæ of the head somites, certain of which also appear in Figure 15. These indicate clearly the sensory rings of the somites in that region, and so aid in the determination of the external limits of the somites. The eye is clearly derived from one of the segmental organs of somite III. (ring 2), as the position of its nerve indicates. This view is confirmed by a comparison with the conditions existing in G. heteroclita and G. elegans.

3. Glossiphonia elongata sp. nov.

Plate 6.

a. HABITAT, FORM, SIZE, COLOR.

This leech first came to my notice in September, 1898. While collecting G. stagnalis from Spy Pond, near Cambridge, I found three or four leeches which, although of about the same size as stagnalis and occurring in similar situations, at once attracted my attention because of their more slender bodies and the peculiarities of their movements. These animals were carefully preserved, and diligent search was made the following spring for more. This search, however, was fruitless; but in September, 1899, I was fortunate enough to find quite a number of individuals in a pool near Fresh Pond, Cambridge, some of which I have since kept alive in aquaria for several months.

The body is less flattened dorso-ventrally in this species than in any other Glossiphonia known to me, being sub-cylindrical in cross-section. It is extremely slender, even when contracted, and both head and acetabulum are small (Figure 27, Plate **6**). This species does not roll itself into a ball, as other species do, when disturbed. Instead, it writhes about or twists itself into knots like an earthworm. In aquaria it moves little from place to place, but, attached by its weak posterior sucker, extends its snake-like body searching hither and thither as for a place of concealment, or, losing its attachment, seems unable to regain it and writhes helplessly like an earthworm on a smooth surface.

The largest individuals which I have examined measure as follows: —

Length, fully extended, 25 mm.; partially contracted (as in Figure 27), about 10 mm.

Width, fully extended, less than 1 mm.; partially contracted (as in Figure 27), about 1.5 mm.

Color. — The anterior and marginal parts of the body are very clear and transparent. The rest of the body is usually of a pale yellowish-white color when the animals are first collected, but changes to a rusty yellow or pale orange color if they are kept in well-lighted aquaria for a few days. The color is due to the presence in the deeper parts of the body of rounded reserve-food cells, similar to those described as occurring in G. stagnalis. Apparently the nature of the granules in the reserve-food cells changes under the influence of daylight, so that by reflected light they appear pale orange instead of yellowish-white, the color which they have when first collected.

Superficial pigment cells of the branched type, described as occurring in G. stagnalis and other species, appear to be entirely wanting in G. elongata.

Fat cells occur in abundance in the deeper parts of the body, the contained oil drops being perfectly clear and transparent, as in G. stagnalis and G. fusca.

b. RINGS, SOMITES, EYES, SUCKERS.

The *skin* is very smooth and entirely free from papillæ.

External rings, broad and smooth, usually indistinct in the head region (somites I.–IV., Figure 23). Number of rings, 62 between oral sucker and anus (somites V.–XXVII.).

Notwithstanding the indistinctness of the rings in the head region, favorable preparations, like that represented in Figure *B*, show that the composition of somites I.–IV. is practically the same in this species as in G. heteroclita (Plate **5**) and G. fusca (Plate **4**). Somites I. and II. are uniannulate; somites III. and IV. biannulate, the anterior rings being broader and corresponding to rings 1 and 2 of a typical somite taken together.

Somite V. is likewise biannulate in this species, just as in G. stagnalis (Figure *B*; compare Plate **1**, Figure 3); in all the other species with which this paper deals, somite V. is triannulate.

Somites VI.–XXIV. (Figure 27) are triannulate, as in all other known species of this genus. Somites XXV.–XXVII. are reduced each to a single ring, a condition found in the other species described only in the case of somite XXVII., somite XXV. being always biannulate, and somite XXVI. usually so.

Eyes, two, situated about as in G. stagnalis, just posterior to the mouth, between somites III. and IV. (Figure 23). The eyes are separated from each other by a considerable space, as in G. stagnalis (Plate **2**, Figure 4) and G. fusca (Plate **4**, Figure 16). The pigment associated with them is usually small in amount; often it is wanting altogether.

The *oral sucker*, as in the other species described, lies within the limits of somites I.–IV. The *mouth* lies about in its centre (Figure 23, Plate **6**; Figure *B*). The *posterior sucker* (*act.*, Figures 24, 27) is extremely small and weak. In position it may be described as terminal rather than ventral (the position which it occupies in other species).

c. Reproductive Organs.

The *genital pores* have the same position as in G. stagnalis and G. fusca; the male (*po.* ♂, Figure 27), between the first and second rings of somite xii., the female (*po.* ♀, Figure 27), between the second and third rings of the same somite.

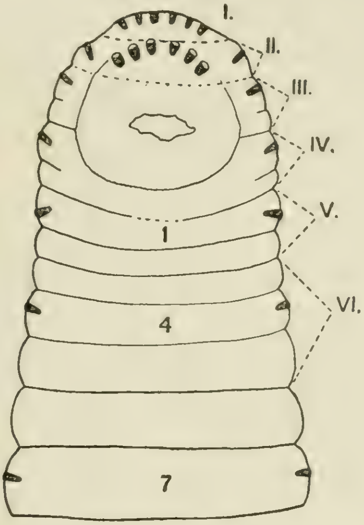

Figure *B.* — *G. elongata.* Ventral view of head end, showing annulation of head somites and position of marginal sensillæ.

Testes (*te.*, Figure 27), six pairs placed intersegmentally in somites $\frac{\text{XIII.}}{\text{XIV.}}-\frac{\text{XVIII.}}{\text{XIX.}}$, as regularly in the genus.

The *ovaries* (*oa.*, Figure 27) have the typical structure and position which they possess in other species (see p. 25). The eggs and egg-laying of this species I have not observed.

d. Digestive Tract.

The *mouth* (*or.*, Figure 23, Figure *B*) opens about in the middle of the oral sucker. The *proboscis* (*pr'b.*, Figure 27) commonly extends over about four somites (viii.–xi.). The *salivary glands* (*gl. sal.*) are found chiefly in somite xii., though a few may lie in the adjacent somites, xi. and xiii. About thirty good-sized gland cells are found in either half of the body. In size, number, and position the salivary glands of this species resemble those of G.

stagnalis more closely than those of any other species (compare Figures 1 and 27).

The *crop* (*i'glv.*, Figure 27), as in G. stagnalis, bears a single pair of diverticula, which arise in the middle of somite XIX.; but the diverticula are shorter in this species than in stagnalis, ending usually in somite XX. (compare Figures 1 and 27). The *stomach* (*ga.*), as in all species of Glossiphonia, bears four pairs of lateral diverticula. They arise within the three somites XX.–XXII. All are directed slightly forward. The *intestine* (*in.*) is a simple tube not constricted into distinct chambers proximally as in most species. The *anus* (*an.*, Figure 24) lies just behind somite XXVII.

In the structure of its digestive tract, as well as in the composition of its somites, this species shows a more reduced, simpler condition than is found in any other species known to me, stagnalis coming nearest to it in these particulars.

e. NERVOUS SYSTEM.

On account of the transparency of the body the central nervous system can be studied with ease in this species, either in the living animal or in whole preparations. In the ventral ganglionic chain there are, as in all species of Glossiphonia, twenty-one distinct ganglia. These innervate somites VII.–XXVII. respectively.

The brain (*cb.*, Figures 23, 27; also Figures 25, 26) represents the fused ganglia of the first six somites. The arrangement of its ganglionic capsules is the same as in G. stagnalis and G. fusca (Figures 8, 10, 12, 18). The two ventral capsules of somite VI. (*6*, *6*, Figure 25) are arranged tandem, those of somites I.–V., side by side. The supra-œsophageal commissure lies well back, about over the lateral capsules of somite V. (Figure 26).

4. **Glossiphonia heteroclita** LINNÆUS (1761).

Plate 5; Plate 8, Figs. 35, 36, 38.

Hirudo heteroclita Linnæus (**1761**), H. hyalina O. F. Müller (**1774**); Clepsine hyalina Moquin-Tandon ('**26**).

a. HABITAT, FORM, SIZE, COLOR.

This small and transparent leech is found both in Europe and in North America. Compared with G. stagnalis and G. fusca, it has a proportionally shorter and broader body (Plate **5**, Figures 19, 22; Plate **8**, Figure 38. Compare Plate **1**, Figure 1; Plate **2**, Figure 4); in its movements, it is less active. It is found in ponds and sluggish streams, such as G. stagnalis frequents.

Length of largest individuals, when extended, 13 mm.; at rest, 8–9.5 mm.

Width, extended, 3 mm.; at rest, 4.25 mm.

Color. — The body is in general very clear and transparent, like that of a jelly-fish, but shows great individual variation in the matter of pigmentation.

First, it always has more or less of a golden-yellow tint caused by the presence, in the deeper parts of the body, of large, rounded cells each containing a single yellow oil-drop, which is blackened when treated with osmic acid.[1]

Secondly, there are usually present (but this is the variable element in the pigmentation) irregularly rounded, oval, or even somewhat branched cells, which contain pigment granules either orange, dark-brown, or black in color. These cells are found near the dorsal surface of the animal, and often produce a conspicuous color pattern by their abundance in certain regions (Figure 38, Plate **8**). In their finer structure, cells of this variety are rather closely related to the deep-seated pigment cells (reserve-food cells) found in G. stagnalis and G. fusca; but in respect to position (close to the surface), and occasionally in form (irregular or branched), they approach more nearly the superficial pigment cells ("excretophores," Graf) of the species named.

The pigmented areas which are often produced in G. heteroclita by the superficial pigment cells just described are (Figure 38, Plate **8**), first, a median dorsal, longitudinal band, which, when best developed, extends, with occasional interruptions, from about the seventh somite back to the anus. In the anterior ring of each somite it often broadens out into a trapezoidal form. Secondly, in about the same regions of the body (seventh to twenty-seventh somites), the anterior ring of each somite may be marked by a transverse, pigmented line, most conspicuous a short distance from the margin of the body, from which point it extends inward toward the trapezoidal, broad part of the median vitta, but rarely joins it.

Apáthy ('**88**) has recognized as a distinct variety (striata) animals which have the transverse markings just described. It must be said, however, that one can find in a lot of animals collected from the same locality all gradations between forms with no pigment at all (of the superficial sort) and those having a median vitta and well-defined transverse striations.

b. Rings, Somites, Eyes, Suckers, etc.

The *surface* of the body is rather smooth, being only slightly rougher than that of G. stagnalis.

External rings, rather inconspicuous, particularly in the head region, where it is often difficult to determine their number and limits accurately.

Number of preanal rings, seventy, counting as a single ring each of the somites I., II., XXVI., and XXVII., Figure 19. This number may be increased, if one counts subdivisions occasionally visible in some of the rings at the ends of the body.

Somites I. and II., as just indicated, are commonly uniannulate (Figures 35, 36, Plate **8**); but somite II. is sometimes subdivided by a transverse furrow (as shown in Figure 20, Plate **5**).

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[1] Fat cells are also found in the deep parts of the body of G. stagnalis, G. fusca, and G. elongata, but the contained oil-drops are in those species perfectly clear and transparent, so that they do not have the effect of pigment cells, as do the fat cells of G. heteroclita.

Somite III., within the anterior part of which lies the mouth (*or.*, Figure 20), is ordinarily biannulate, as are also somites IV. and XXV. (Figures 19, 35, 36). But in the section shown in Figure 20, ring 3, the anterior annulus of somite III., appears conspicuously subdivided, a rather unusual condition. On account of the obliquity of the section, the first three somites appear in that figure a little too long in proportion to their vertical dimensions. The sensilla shown in the anterior portion of ring 3 in Figure 20 is probably not one of the segmental sense-organs, for it is found on the wrong half of ring 3.

Somites V.–XXIV. are triannulate, as in G. fusca.

Somites XXVI. and XXVII. (reckoned as uniannulate) usually appear divided at the margin only into a broader anterior and a narrower posterior part.

Compared with the species already described, the somite composition of G. heteroclita is about the same as that of G. fusca, somite abbreviation being less extensive in these species than in stagnalis and elongata.

Eyes, usually six, the anterior pair small and generally, though not always, close together in ring 5 (Figures 35, 36, Plate **8**). Sometimes this pair of eyes lies in ring 6; occasionally the pigment of one or both eyes is wanting altogether.

The second and third pairs of eyes are most often found in rings 7 and 8 respectively, but one pair or the other or both may lie a little anterior or a little posterior to the ordinary position (compare Figures 35 and 36).

The first and second pairs of eyes are directed forward and toward the side; the third pair is directed backward and toward the side (Figures 20, Plate **5**; Figures 35, 36, Plate **8**). The eyes in this species seem to belong to somites III., IV., and V., respectively (Figure 20); but it is possible (though I think hardly probable) that a more careful study of the nerve connections would show that in this species, as in G. elegans (Figure 29, Plate **7**), they have been derived from the sensillæ of somites II.–IV. If so, the eyes have undergone a farther displacement backward in this species than in the case of G. elegans (compare Figures 20 and 29).

Oral sucker, formed by somites I.–IV. (Figure 20).

Mouth (*or.*, Figure 20), in the anterior part of somite III., usually a little anterior to the first pair of eyes.

Posterior sucker, as in other species, slightly longer than broad (Figure 19).

c. REPRODUCTIVE ORGANS.

Male and female genital ducts open between the first and second rings of somite XII. (rings 28 and 29, Figure 19) by a common pore, a condition peculiar, I believe, to this species.

Blanchard ('**94**) is certainly in error in describing the position of the genital pores as follows: "Porus genitalis masculus inter annulos 25–26, vulva inter annulos 27–28 hians."

Testes (*te.*, Figure 19), six pairs placed intersegmentally in somites $\frac{\text{XIII.}}{\text{XIV.}}-\frac{\text{XVIII.}}{\text{XIX.}}$. The terminal part of the vas deferens (ejaculatory part) is unusually stout and thick in this species and runs forward to the middle ring of somite XI. before turning sharply backward toward the genital pore (compare Figure 19 with Figures 4, 13, 27, and 28).

The *eggs*, which in the vicinity of Cambridge are laid in May or June (at about the time G. fusca is laying), are whitish in color and are attached *singly*, not in groups as in the other species described, to the under side of the body (Figure 22). The eggs are of about the same size as those of G. stagnalis. The number laid varies greatly with the size of the individual, the observed extremes being eleven and sixty-five. Figure 22 shows in ventral view a large individual bearing forty-five eggs, each enclosed in a separate delicate sac which serves to attach it to the under side of the body.

d. DIGESTIVE TRACT.

The *mouth* has the position most common in the genus, in the anterior part of somite III. (Figure 20).

The *proboscis* (*pr'b.*, Figure 19) is long and the *œsophagus* correspondingly short. The former ordinarily extends over somites IX.–XII. and part of XIII., and the latter ends in the anterior part of somite XIV., where the crop commences.

The *salivary glands* (*gl. sal.*, Figure 19) are large and distributed often through as many as seven or eight somites, usually somites XI.–XVII.

The *crop* (*i'glv.*, Figure 19) bears six pairs of strongly developed lateral diverticula, a pair arising in the middle of each of the somites XIV.–XIX. Some or all of the first five pairs may be bilobed distally, and each of the sixth pair, which are very long, and extend back into somite XXIII., bears about five secondary, lateral diverticula, which come off metamerically in somites XIX.–XXIII.

The *stomach* (*ga.*, Figure 19), with its four pairs of lateral diverticula, lies within somites XIX.–XXII.

The *intestine* (*in.*, Figure 19) begins about in somite XXII. and extends back to the anus just behind somite XXVII. Proximally it consists of one or two chambers limited by valve-like constrictions. Posterior to this it gradually narrows backward.

e. NERVOUS SYSTEM.

The brain (*cb.*, Figure 19) lies about in the eighth somite. The arrangement of its ganglionic capsules is peculiar in one respect. The ventral capsules of the last brain neuromere (Figure 21) lie side by side, not tandem as in the other species described in this paper. In other respects the arrangement of capsules is the same as that found in G. stagnalis and G. fusca (Figures 8, 12, 16, 18). In the individual whose brain is represented in Figure 21, the most ventral and posterior capsule of neuromere I. had a horn-like process extending back laterally into contact with the lateral capsules of neuromere III.; this condition, however, appears to be unusual.

5. Glossiphonia elegans Verrill (1872).

Plate 7; Plate 2, Fig. 5; Plate 3, Fig. 11.

Clepsine elegans Verrill ('**72**); (?) C. pallida Verrill ('**72**); C. patelliformis Nicholson ('**73**).

a. Habitat, Size, Color.

This species is very closely related to the European G. complanata L. and G. concolor Apáthy. Blanchard ('**94**), indeed, considers it identical with G. complanata L. and regards G. concolor Apáthy as merely a variety of the same species. However, both Apáthy ('**88**) and Oka ('**94**) testify to the perfect distinctness of G. complanata and G. concolor, which occur together in Europe. I have myself compared animals of the species to be described with alcoholic specimens of G. complanata from Zürich, Switzerland, and find certain small but constant differences between the two. I shall therefore describe the animals which I find here in the vicinity of Cambridge under the name proposed by Verrill in 1872, recognizing, however, that they are very closely related to the two European species (or varieties) named.

G. elegans (Plate **7**) is found in localities similar to those frequented by G. stagnalis, often in company with that species. It is considerably larger, being much broader and thicker in proportion to its length, though scarcely longer.

In its movements it is more sluggish, resembling closely the small G. heteroclita in that regard. It adheres to the side of the aquarium with a tenacity displayed by no other of our species except G. parasitica.

The form of the body at rest is elliptical.

The largest individuals which I have collected measure, when alive, as follows: —

Length, fully extended, 28 mm.; at rest, 14–18 mm.

Width, fully extended, 5 mm.; at rest, about 7 mm.

Color. — Small individuals are usually of a bright, transparent green color. Adult animals, viewed with the naked eye or through a hand lens, appear of a reddish or greenish brown color, and are darker above than below.

The head is colorless. The dorsal surface of the body is marked with numerous small circular white spots, about the width of a body-ring in diameter. These spots are so placed as to form transverse and longitudinal rows, just as do the similar spots of G. fusca. The transverse rows fall on the sensory (middle) rings of their respective somites, each row containing seven spots, when the full number is present. Each of these seven spots falls in a different longitudinal row, there being three pairs of rows arranged symmetrically with reference to an unpaired (median) row, exactly as in G. fusca. The paired rows may be designated respectively *paramedian, intermediate*, and *marginal*, for they occupy practically the same position on the body as do the rows of white spots in the case of G. fusca, and the rows of papillæ in that of G. parasitica (Figure 6).

In addition to the spots which fall into rows as just described, a few spots are usually found scattered more or less irregularly over the surface of the body.

Two interrupted brown lines (Figure 30) appear in a paramedian position on the dorsal surface, the interruptions being due to the segmentally arranged white spots of the paramedian rows. A pair of similar, though fainter, dark lines is found on the ventral surface; but they are farther apart, including between them about the middle third of the ventral surface. The dorsal paramedian lines include between them (in the middle of the body) about one fourth of the width of the dorsal surface, which part is usually rather more heavily pigmented than the more lateral portions.

A median, clear, unpigmented band extends the entire length of the body on the ventral surface. The median row of light spots on the dorsal surface often run together in the posterior third of the body, forming a continuous light vitta.

Examining more minutely into the coloration of the animal, one finds that it is due to the same two classes of cells as produce the coloration of most other species: first, pigment cells proper, — "excretophores," Graf; and secondly, reserve-food cells.

The pigment cells proper, as in other species, occupy a superficial position in, or immediately underneath, the epidermis. They are stellate or richly branched, and are more abundant on the dorsal than on the ventral surface; in small individuals they are almost entirely wanting. The pigment in immature animals is a rust-colored or dull reddish-brown, but in full-sized animals it is usually dark-brown.

There is no pigment anterior and lateral to the eyes, nor in the white spots already mentioned. The pigment is more abundant than elsewhere in the paramedian dark lines, indeed its abundance there *produces* those lines.

The reserve-food cells in this species, as in G. fusca, are of two forms: first, the ordinary form of large reserve-food cell distributed irregularly through the deeper parts of the body; secondly, a special form of reserve-food cell, smaller, and more superficial in position, and found only in the white spots already described.

The *ordinary reserve-food cells* are large and rounded in outline, often attaining a diameter of forty mikra or more. They contain rounded granules of a bright green color both by reflected and by transmitted light. It is this form of cell which gives to the small, immature individuals their green color, and often imparts a greenish tone to the brown-colored adults.

The *special form of reserve-food cell* agrees closely both in appearance and in distribution with the similarly designated structures of G. fusca. It is found, as already stated, only in the white spots of the dorsal surface; cells of this kind occur in a group of from two to a dozen or more each, situated in the centre of a white spot, just underneath the epidermis. By reflected light they are of a light lemon-yellow color; by transmitted light, greenish-brown.

Each of the white spots in the paired rows contains an inconspicuous, low rounded papilla (much less prominent than are the papillæ of G. complanata, so far as my observations go).

The median row of white spots is less well developed than are the paired rows; in the four or five somites immediately anterior to the anus, it is commonly replaced by a continuous, median, clear vitta, within which is seen a narrower band of the lemon-yellow reserve-food cells.

Obviously the color pattern of this species resembles very closely that of G. fusca, although in a majority of characters the animal is more closely related to G. parasitica.

b. SURFACE, RINGS, SOMITES, EYES, SUCKERS.

The *surface* of the body is rather rough, owing to the strong development in this species of the integumental sense-organs described by Bayer (**'98**). It does not, however, bear conspicuous papillæ, as is the case with G. parasitica and the European G. complanata. The low, rounded papillæ which are found in the paired longitudinal rows of white spots are much smaller than the similarly placed papillæ of G. complanata. In this particular G. elegans seems to agree with G. concolor (see Apáthy, **'88**, page 771).

External rings, as a rule, rounded and distinct, *less convex and not pointed as are those of G. complanata*, sixty-eight in number, distributed as follows: —

Somites I.–IV. uniannulate; but the boundary between rings 1 and 2 is often inconspicuous (compare Figures 28, 29, 30), approaching the condition found in G. stagnalis, where somites I. and II. form a single broad ring, which, however, is sometimes divided by a shallow transverse furrow (Figures 3, 7).

Somites V.–XXIV. triannulate, but the condition of somite V. is peculiar. Its anterior annulus (*5*, Plate **7**, Figures 28–31) is commonly narrow and imperfectly separated from the following (sensory) annulus (*6*). This case illustrates well the initial step in reduction (or final step in elaboration, p. 33) of the triannulate somite. It represents an intermediate stage between the biannulate and triannulate condition of somite V. seen respectively in G. stagnalis (Figure 7, Plate **3**) and G. heteroclita (Figure 20, Plate **5**).

Somite XXV. is biannulate (Figure 28), but the furrow between its two annuli is often inconspicuous. Somites XXVI. and XXVII. are commonly uniannulate, though notched at the margin of the body, which fact shows that the final step in somite reduction (or initial step in somite growth) is not yet accomplished in the case of these somites.

Eyes, six, in two parallel rows close together, in rings 3 and 4 (Figure 30). Sometimes the first pair of eyes lies partly in the posterior half of ring 2 (Figure 29). The middle pair is the largest of the three; the anterior pair, the smallest. The first two pairs are directed obliquely forward, the last pair obliquely backward; all are turned away from the median plane (Figures 29, 30). From the relation of the eyes to the nerves connected with the metameric sensillæ (Figure 29), it is plain that the three pairs of eyes have been derived from the sensillæ of somites II., III., and IV. respectively. It is further evident that the single pair of eyes found in each of the species stagnalis, fusca, and elongata corresponds with the middle (largest) pair of eyes of this species, the pair belonging to somite III.

The *oral sucker*, as in the other species described, lies within somites I.–IV. (Figures 29, 31).

c. Reproductive Organs.

Male genital pore (*po.* ♂, Figure 28), between somites XI. and XII. (rings 25 and 26), a position one ring anterior to that of the same structure in the species already described.

Female genital pore (*po.* ♀, Figure 28), between the second and third rings of somite XII. (rings 27 and 28), the usual position of this structure in the genus.

Testes (*te.*, Figure 28), ten pairs. The anterior six pairs occupy the same positions as the testes in the species already described, being placed intersegmentally in somites $\frac{\text{XIII.}}{\text{XIV.}}-\frac{\text{XVIII.}}{\text{XIX.}}$. The remaining four pairs occur immediately behind those already mentioned; the most anterior one, between the last crop and first stomach diverticulum, in somites $\frac{\text{XIX.}}{\text{XX.}}$; the other three between successive stomach diverticula, and like them separated by rather less than metameric intervals. No other species of Glossiphonia known to me, except the European G. complanata, has normally a greater number of testes than six pairs. In that species likewise the testes number ten pairs placed exactly as in elegans. This is one of several facts showing the very close relationship of the two species named. The last one or two pairs of testes are less constant in their occurrence than those farther forward.

Eggs are laid by G. elegans, in the vicinity of Cambridge, in April, May, or as late as June. The temperature of the water in the spring undoubtedly exercises considerable influence in determining the time of egg-laying. Individuals brought into the laboratory on March 27, 1898, laid eggs nine days later. On April 29, 1900, animals of this species bearing eggs were collected from Alewife Brook, Cambridge, though G. stagnalis, found with them, apparently had not yet laid its eggs. The eggs are dull pinkish white in color and are borne on the under side of the body in from three to six large clusters, which are rather easily detached from the body, if the animal is disturbed. Each cluster contains a considerable number of eggs, often as many as twenty or twenty-five, enclosed in a delicate sac. The sacs are not arranged symmetrically in two parallel rows, as in G. stagnalis and G. fusca, but quite irregularly, a sac being attached either in the median plane of the body or to one side of it, as the case may be.

d. Digestive Tract.

The *mouth* is situated well forward in somite III., anterior to the eyes, or at least anterior to the last two pairs of eyes (Figures 29, 31).

The *proboscis* (*pr'b.*, Figure 28) is long, extending over somites VIII.–XII. There is practically no œsophagus, as I have used the term, for the pharyngeal sac containing the proboscis extends back almost to the beginning of the crop.

The *salivary glands* are numerous, often reaching seventy-five or more in number in each half of the body. They are scattered usually through somites XI.–XVIII. In Figure 28 they are represented as relatively a little too small.

The *crop* (*i'glv.*) bears *seven* pairs of large, lateral diverticula directed backward and often lobed distally. They arise in somites XIII.–XIX., always in the middle of a somite, as in the other species described. The last pair of crop diverticula is, as usual, the largest of all; it may extend back through three or four somites, giving off secondary lateral diverticula metamerically, as shown in Figure 28. Often, however, when the crop is empty, the last pair of diverticula is little longer than the preceding pair.

The *stomach* (*ga.*, Figure 28) bears, as in other species, four pairs of diverticula, which arise within the three somites XIX.–XXI. The *intestine* (*in.*) extends through the six remaining somites, consisting proximally of two distinct chambers limited by valve-like constrictions and usually situated in somites XXII. and XXIII. Distally it is a gradually narrowing tube terminating at the anus just behind somite XXVII.

e. NEPHROPORES, NERVOUS SYSTEM.

The *nephropores* open ventro-laterally, a little anterior to the middle of the sensory ring of a somite. The number of nephridia has not been determined for this species.

The *brain* (*cb.*, Figures 28, 30) lies for the most part in somite VII. The arrangement of its ganglionic capsules (Figure 5, Plate **2** ; Figure 11, Plate **3**) is usually similar to that found in the brain of G. stagnalis and G. fusca, but the capsules are not so closely crowded together, and the supra-œsophageal commissure lies well forward, not being carried back over the middle of the brain as in G. stagnalis (Figure 12). The less crowded condition of the capsules in this species (Figure 5) explains an abnormality in their arrangement observed in the brain of a single individual out of several examined; the two ventral capsules of somite III. (usually found side by side as in G. stagnalis and the other species already described) were in this case arranged tandem, just as in ganglia in unabbreviated somites.

Comparing the conditions of the brain capsules in the several species described in this paper, one may say that the larger the leech is, the less are its capsules crowded. This fact seems to indicate that the capsules, and probably the individual ganglion cells also, do not increase in size proportionally with the growth of the leech. This is certainly true of the development of the individual, if not also of the race, for in the very young leech the ganglia of the nerve chain occur in close succession with scarcely any intervening space, whereas in the adult they may be separated by a distance of two rings or even more.

6. Glossiphonia parasitica Say (1824).

Plate 1, Figs. 2, 3*a*, 3*b*; Plate 2, Fig. 6; Plate 8, Figs. 32, 33, 37.

Hirudo parasitica Say ('**24**); Clepsine parasitica Diesing ('**50**); C. plana Whitman ('**91**^{a}); ? C. chelydræ Whitman ('**91**^{a}).

a. HABITAT, FORM, SIZE.

This large and conspicuously colored leech is the commonest and most widely distributed of our North American species of Glossiphonia. It is often found adhering to the bodies of turtles, whose blood it sucks, or underneath stones in pools and streams frequented by turtles. It is referable to the genus Placobdella Blanchard ('**94**), if one recognizes the validity of that genus. In it are included probably several forms which because of their close relationship I choose to call varieties. One of these has been carefully described by Whitman ('**91**^{a}) under the name "Clepsine plana." In what follows I hope to supplement that description and add the description of another form which is commonly found associated with it. The two varieties agree completely, so far as I can determine, in form, size, and constitution of somites, but can be distinguished in my collections by constant differences in roughness of surface and in color pattern.

In *general form* the body in this species is very broad and flat. Whitman describes it correctly in the case of large individuals as "ovate-elliptical in contraction, emarginate posteriorly." In the case of small individuals, however, or of large individuals well extended, the emarginate condition is not present (Figure 6, Plate **2**; Figure 37, Plate **8**; Figure *C*, p. 56). The dimensions given by Whitman for the largest individuals, I can substantiate: "*Length at rest*, 5–6 cm.; width, 2.6 cm." I have an alcoholic specimen (var. rugosa) from Lake Chautauqua, N.Y., which measures 5.6 cm. in length, and 3 cm. in width. Another (var. plana) taken from a turtle brought from the Illinois River measures 5.5 cm. in length, 2.3 cm. in width. A living specimen (var. plana) taken from a snapping turtle (Chelydra serpentina) captured near Cambridge, Mass., measures at rest 5.8 cm. in length, 2.1 cm. in width. Whitman says further: "*Length in extension*, 8.5 cm.; width, 1.8 cm." My living Cambridge specimen attains in extension a length of about 7.5 cm., in which condition its greatest width is 1.5 to 1.7 cm.

b. RINGS AND SOMITES.

The *rings* are distinct except at either end of the body. The furrow between the anterior and middle rings of each somite is, however, less deep than that which separates other rings, for which reason the anterior two thirds of a somite sometimes appears like a single broad annulus, especially at the margin of the body (Figures 2, 3 *b*, Plate **1**; Figure 6, Plate **2**; Figures 32, 33, 37, Plate **8**).

Somites I., II., and XXV.–XXVII. uniannulate (Figures 6, 33, 37), but XXV. and

XXVI. are commonly divided at the margin of the body into a broad anterior and a narrow posterior portion. Somites III. and IV. are biannulate, the broad anterior ring in each case bearing the sensillæ and representing both the anterior and the middle ring of a triannulate somite (Figure 2, III.–VI.). The remaining preanal somites (V.–XXIV., Figure 6) are triannulate, but the posterior annulus of XXIV. is narrower than the adjacent annuli (Figure 6), and the anterior and middle annuli of somite V. are united ventrally while separated by only a very shallow furrow dorsally (*7*, *8*, Figures 2, 3 *b*, Plate **1**. These two cases illustrate the centripetal progress of abbreviation (or arrested development), that part of each terminal triannulate somite being affected which is adjacent to an abbreviated somite.

In Figure 32, Plate **8**, is shown a rather unusual condition, the apparent disappearance of the furrow separating somites II. and III.[1]

The total number of *preanal rings* is sixty-nine, counting somites I., II., and XXV.–XXVII. as uniannulate, III. and IV. as biannulate, and V.–XXIV. as triannulate (Figure 6).

c. EYES, MOUTH, ORAL SUCKER.

The *eyes* appear in the living animal, or in whole preparations, as a single pair closely united and situated in rings 3 and 4 (somite III.). See Figure 6, Plate **1**; and Figures 32, 33, Plate **8**. An examination of sections, however, particularly of young individuals, shows that there are really three distinct pairs of eyes present, there being a small rudimentary pair anterior, and another still more rudimentary posterior to the principal pair of eyes, exactly as shown for "C. hollensis" by Whitman ('**92**, Figure 6).

All three pairs of eyes[2] are partially imbedded in a common pigment mass, the anterior and middle pairs being directed forward, the posterior pair backward, just as in G. elegans and G. heteroclita (Figures 20, 29). The largest

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[1] A similar condition is figured by Whitman ('**91**a) in his Plate 15, Figure 1. In his text, however, Whitman says (p. 412): "In front of the eyes I was unable to discover any distinct rings. In another species *C. chelydræ*, from Wisconsin, there are three narrow rings in front of the eyes; and the first is marked by the usual metameric sense-organs. Although no metameric sense-organs were recognized in front of the eyes in *C. plana*, the correspondence of other metameric characters in the two species is sufficiently close to enable me to identify the ocular rings as equivalents. The preocular part of the head is, therefore, probably equivalent to the first somite of *C. chelydræ*, and is so numbered in Figure 1."

In view of Whitman's subsequently published studies on "The metamerism of Clepsine" ('**92**), I think he unquestionably would now recognize *two* preocular somites both in "C. plana" and in "C. chelydræ"; at any rate, that is the number found in the species which I am describing (Figure 2, Plate **1**). Since Whitman has pointed out no other difference between his "plana" and "chelydræ" than the uncertain one of preocular rings, I consider that their specific distinctness remains to be established.

[2] Only the largest (middle) pair of eyes appear in the section shown in Figure 2.

(middle) pair is closely united with sensillæ situated in the first ring of somite III. (Figure 2), a fact which Whitman ('**92**) established for "C. hollensis" and which I can completely confirm for the species under discussion (Figure 2).[1]

Whitman ('**92**) further established the fact that the anterior pair of eyes in "hollensis" originates in connection with the sensillæ of somite II. He gives no statement as to the origin of the posterior pair. Comparison with G. elegans (Figure 29), however, leads me to regard this pair as probably derived from the sensillæ of somite IV. If so, the condition of the eyes in parasitica can be derived in its entirety from that found in G. elegans by supposing that both the anterior and the posterior pairs of eyes have become rudimentary and been brought close to the large middle pair.

The *mouth* (*or.*, Figure 2) apparently lies between somites I. and II.; in other species it lies farther back, usually in the anterior part of somite III. The *oral sucker* is formed by somites I.–IV., as in other species.

d. REPRODUCTIVE ORGANS.

The *genital pores* are situated in this species exactly as in G. elegans; the male (*po.* ♂, Figure 3 *b*), between somites XI. and XII. (rings 27 and 28); the female (*po.* ♀), between the middle and posterior annuli of somite XII. (rings 29 and 30).

Testes, six pairs situated intersegmentally in somites $\frac{\text{XIII.}}{\text{XIV.}}-\frac{\text{XVIII.}}{\text{XIX.}}$, the usual position in the genus.

The *eggs* are large, white, and opaque. In the vicinity of Cambridge they are laid in May and June, perhaps also in July. In the case of those animals which laid in the laboratory, the eggs appeared to be attached loosely in a single group of fifty or more to the side of the aquarium, rather than to the body of the leech as is the case in the other species studied. The leech remained closely arched over the eggs, — a position from which it was removed only with great difficulty.

e. DIGESTIVE TRACT.

The digestive tract resembles very closely that of G. elegans, but has one strikingly distinctive feature: the *salivary glands* (*gl. sal.*, Figure 3 *b*), instead of being distributed through several somites in the crop region, are closely aggregated into two compact groups in each half of the body, these groups lying symmetrically, a pair on either side of the proboscis, within somites IX.–XI.

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[1] On account of this and other close structural agreements with "C. hollensis" as described by Whitman ('**92**), I was for some time inclined to regard that name as well as "chelydræ" as a synonym with parasitica, and I have so treated it in a recent publication (Castle, **1900**). Professor Whitman, however, has subsequently informed me in a letter that in hollensis "there are several pairs of pigmented eyes behind the pair usually recognized as 'eyes.' These are quite conspicuous in the living leech, and I have never seen any such feature in other Clepsines." This being so, it is probable that hollensis should rank as a distinct species.

The *crop* bears *seven pairs* of lateral diverticula, as in G. elegans and the closely related European G. complanata, with both of which this species has many points in common. The first pair of diverticula arise in the anterior or middle part of somite XIII. and are two or three lobed, the anterior lobe being prolonged forward through somites XII. and XI. The five following pairs of crop diverticula arise in the middle of somites XIV.–XVIII. respectively, and are usually bilobed distally. The last (seventh) pair of crop diverticula extend far back of their origin in somite XIX., often into somite XXIII. They give off secondary lateral diverticula, a pair in each of the somites through which they extend.

The crop diverticula are often a conspicuous feature of this species when viewed in a living condition from the ventral side of the animal, for numerous large green chromatophores aggregate about the crop and show through the clear ventral body wall the form of the crop outlined in green.

f. NEPHROPORES, NERVOUS SYSTEM.

The *nephropores* (*nph'po.*, Figure 3 *b*) open ventrally, anterior to the middle of the sensory ring of a somite, as stated by Whitman (**'91**^{a}). They are present in the eighth and all the following triannulate somites.

I have nothing new to add to Whitman's (**'92**) excellent account of the *central nervous system.* It is important to notice, however, the arrangement of the ventral capsules in the brain region (Figure 3 *b*). Those of neuromeres III.–VI. *all lie in a single row* in the median plane; that is, have what I have called the tandem arrangement. The ventral capsules of neuromere II. (*2*, *2*, Figure 3 *b*) have the side-by-side position found in all the species examined by me.

Figure 3 *a* is a dorsal view of the brain and shows that the supra-œsophageal commissure in the species lies far forward in what may well be regarded as its primitive position.

The less crowded condition of the brain capsules in this as compared with other species is interesting, as showing that the smaller the leech is, the more crowded are its brain capsules likely to be (compare page 50).

g. PAPILLÆ, COLORATION.

I have reserved to the last, in describing this species, the discussion of papillæ and coloration, for it is on the basis of these characters alone that I am able to distinguish two varieties, plana and rugosa, which I find associated together, but apparently without intergrading forms, in collections from Cambridge, Mass., Lake Chautauqua, N. Y., Lake Forest, Ill., and Wellsville, Kan., a very wide range extending across the Mississippi valley and the Atlantic seaboard.

(1) *Var. plana Clepsine plana* Whitman, **'91**^{a}).

This variety has a relatively smooth skin, which bears dorsally small dome-shaped *papillæ,* the most conspicuous of which are placed as indicated by stars in Figure 6, Plate **2**. They include five longitudinal rows of papillæ found on the middle (sensory) annuli of usually all the triannulate somites. These rows may be designated, from their position, median, marginal, and intermediate, the first named being unpaired, the other two paired.

A row of papillæ is found also between the median and each intermediate row, but these papillæ are situated not on the middle, but on the *posterior* annulus of each of the somites from about VIII. to XXII. inclusive (Figure 6). These will be designated paramedian rows.

The most conspicuous papillæ of somites XXV.–XXVII. are usually placed as indicated in Figure 6. They consist, first, of a continuation of the marginal rows back to the anus; secondly, of two rows of three papillæ each, placed one on either side of the median plane and too near it to fall in the paramedian rows found farther forward.

Other less conspicuous papillæ occur on the dorsal surface of the body and posterior sucker, but no papillæ are found on the ventral surface of the animal.

The general *color* of the body above is brown variegated with yellow, orange, and green. Light areas of yellow or pale orange form: —

I. A median vitta extending from the anterior end of the body back to somite XXV., usually without interruption, but not always so, and expanding commonly at six places, namely, (1) in somites VI. and VII. (Figure 32, Plate **8**); (2) in somite IX.; (3) in somites XII. and XIII.; (4) in somites XV. and XVI.; and (6) in somite XXII. (and the posterior part of somite XXI.). The median row of papillæ already described falls entirely in the median light vitta. In somites XXV.–XXVII. both vitta and papillæ become double, dark pigment being found along the median line back to the anus, usually behind it also quite to the posterior margin of the acetabulum. The double (or paramedian) light vitta of somites XXV.–XXVII. contains the three pairs of papillæ shown in Figure 6, Plate **2**; it may or may not be continuous with the median light vitta farther forward.

II. Throughout the greater part of the body the papillæ of the intermediate rows lie each in an irregularly rounded light spot. The successive spots of each half of the body may become confluent so as to form an irregular, frequently interrupted, longitudinal band.

III. The margins of the body are conspicuously marked with metameric light spots from about the third or fourth somite back to somite XXV. Some idea of the form and position of these spots may be obtained from an examination of the stippled areas in Figure 6, Plate **2**, and Figure 32, Plate **8**. Each spot is typically V- or U-shaped and is placed on the adjacent non-sensory rings of two successive somites. The usually hollow centre of the V or U is formed by a spot of brown sometimes bordered with orange. The margin of the sensory ring is generally darker in color than its more median parts, so that it is strongly in contrast with the metameric light spots which it separates.

The posterior sucker is decorated with radially placed triangular light spots (Figure 6) resembling the marginal spots of the body. Other irregularly rounded light spots may be found on the dorsal surface of the body in light-colored individuals, usually associated with certain papillæ.

There is a certain correlation in the development of light spots in different parts of the body; an animal which has a well-developed median vitta will also have conspicuous marginal and intermediate light spots and vice versa.

The ventral side of the body is much lighter in color, marked only by a few longitudinal bands of dull brown or greenish brown. The number of these bands is either eleven or twelve according as there is present, in addition to five pairs of bands laterally placed, a single broad median band or a pair of narrow paramedian bands separated by an irregular median clear band.

From the under side of the body one can often see in living animals the green pigmented crop diverticula showing through the semi-transparent body.

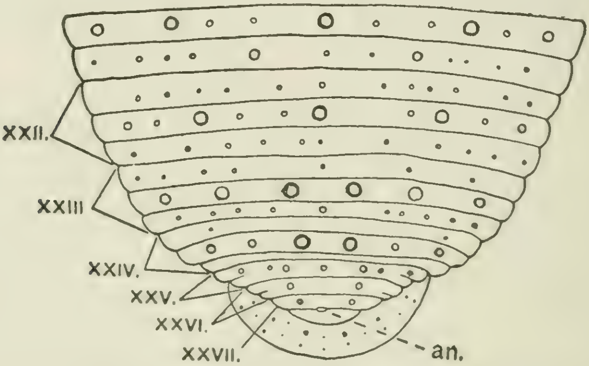

FIGURE *C.* — *G. parasitica, var. rugosa.* Dorsal view of posterior part of body, showing position and approximate relative size of papillæ. From a Cambridge, Mass., individual.

(2) *Var. rugosa, var. nov.*

The dorsal surface of the body is much rougher in this variety, the *papillæ* being larger, more numerous, and structurally more complex. Instead of being simple, low, and dome-shaped, the more conspicuous papillæ are extended distally in several divergent whitish points, giving the body a decidedly rough, harsh feeling to the touch in the case of hardened specimens. The larger papillæ are likewise rendered more conspicuous by the fact that they are commonly unpigmented, though placed in a generally dark background.

The arrangement of the principal rows of papillæ on the dorsal surface is similar to that in G. plana, but with the following easily determined and constant difference. In somites XXIII. and XXIV. (Figure *C*), the median row of papillæ becomes inconspicuous or disappears altogether, and a large papilla appears on either side of the median line, on the sensory ring of each somite. The ventral surface is free from papillæ as in plana.

The *color pattern* is somewhat similar to that of plana, but the contrasts are less striking and the colors less brilliant. The general color effect of the dorsal surface is a grayish brown. Marginal spots of light yellow are present, as in plana, on the non-sensory rings, but they are smaller and do not extend so far mesiad from the margin of the body. Practically all the larger papillæ appear as small white spots in a generally dark background.

The median vitta is not a continuous light band as in plana, but is interrupted at regular intervals by spots of a darker color than the general dorsal surface. It begins as a narrow median light band on the head and neck, constricted or sometimes interrupted in the posterior part of somite VI., less often constricted or interrupted in somite V. also. About in annulus 19, somite IX., begins a narrow dark band which continues to the middle of somite XII. Then come alternating light and dark spots, three of each. A light spot extends over four annuli, a black spot over five as follows: Light spots, annuli 29–32 (Figure 6), 38–41, 47–50; dark spots, annuli 33–37, 42–46, 51–55. Another light spot covers rings 56–64 or 65, broadening out posteriorly so as to include the paired papillæ of somites XXIII. and XXIV. (Figure *C*). This is followed by a median dark spot extending back past the anus to the margin of the posterior sucker.

The posterior sucker is marked by alternating light and dark rays, very much as in plana (Figure 6); it also bears papillæ like those of the body farther forward.

Ventrally the body is light gray in color, owing to the presence there of scattered pigment flecks, which, however, are not arranged in longitudinal bands as in plana.

V. MUTUAL RELATIONSHIPS OF THE SPECIES DESCRIBED.

The species described in this paper, with the exception of heteroclita, fall naturally into two distinct groups (Figure *D*, page 58), which may be designated respectively the stagnalis and the parasitica groups. The former includes the three species stagnalis, elongata, and fusca; the latter, parasitica and elegans, with the closely related European species, complanata and concolor. Heteroclita occupies a somewhat isolated position intermediate between these two groups.

As arranged in Figure *D*., the species form a series in which there is from left to right an increasing degree of complexity of structure. This appears from an examination of rugosity, somite structure, crop diverticula, and certain other characters.

In the species of the stagnalis group (1) there is a single pair of eyes derived from the sensillæ of somite III., (2) the genital pores are separated by a single ring, namely, the middle (sensory) ring of somite XII., and

(3) the crop diverticula are simple and never exceed six pairs in number. (4) All three species are small, (5) have relatively smooth skin, and (6) at least two of them bear the eggs in clusters attached symmetrically in a double row to the under side of the body, the condition in the third species being unknown.

In parasitica and elegans (1) there are three pairs of eyes derived respectively from the sensillæ of somites II., III., and IV., (2) the genital pores are separated by two rings, the anterior two rings of somite XII., (3) the crop diverticula number seven pairs and are lobed, (4) the integument is rough and bears papillæ, (5) the attachment of the egg clusters to the body, when such attachment exists, is imperfect and the arrangement of the clusters irregular.

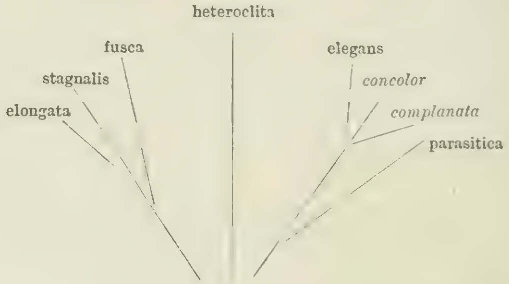

FIGURE *D*. Diagram indicating relationships of the species described.

The European species complanata and concolor are very closely related to elegans, complanata certainly, perhaps also concolor, being intermediate between it and parasitica.

In view of the many points of similarity between parasitica and complanata, there seems to me to be insufficient ground for placing them in distinct genera, as proposed by Blanchard.

Allusion has already been made to the somewhat isolated position of heteroclita. In size and in the character of its integument, it resembles the stagnalis group, likewise in the number of its crop diverticula; in regard to the lobed condition of its crop diverticula, it resembles the parasitica group. In the number of its eyes (three pairs), it likewise resembles the latter group, but the derivation of these apparently is from different somites (III.–V. in heteroclita, II.–IV. in parasitica and elegans.) As regards the position of the genital pores and the way the eggs are borne, it differs alike from both groups.

VI. PARASITES.

Three different endo-parasites, of which I find no notice in the literature, in addition possibly to one already described by Bolsius ('**96**), infest more or less commonly the species of Glossiphonia found in the vicinity of Cambridge, Mass. One of these is a small nematode, another a trematode, these two having been observed in the body of G. stagnalis only; the third is a sporozoön found in at least four of the species described in this paper.

In January, 1898, I first observed a minute *nematode* parasite wriggling about in the central lacunar space of a live G. stagnalis. Another similarly parasitized leech was found upon further search, and a third was found in the following March, the ovary of the host containing at that time full-grown eggs. The parasite in the last-mentioned case lay close to the contractile dorsal blood-vessel, a very common position for it, as subsequent observations showed. In the spring of 1899 several parasitized individuals were collected and studied; and others were observed in the fall of 1899.

The length of the parasite is about the same in the case of all individuals examined; namely, 1.43 mm. In form, the worm is slender and thread-like, being widest near the middle of its body, where it measures 0.027 mm. in breadth. From there it tapers almost imperceptibly toward either end. The posterior end of the body is sharply pointed; the anterior end blunt, its centre being occupied by the very minute, conical mouth.

Examination of a large number of individuals of G. stagnalis in the spring of 1899 showed that between five and ten per cent of the individuals taken from a particular pond, in which the species abounds, contained the nematode parasite. Usually only a single parasite has been observed in the body of a host, but in one case there were three.

The nematode is generally found either coiled up (but not encysted) or wriggling about in the central lacuna (body cavity), in the middle or toward the posterior end of the body. The presence of the parasite does not seem seriously to inconvenience its host, for the parasitized individuals are as large and well developed as those free from parasites, and contain sexual products in equal abundance.

Parasitized individuals were kept in aquaria for several weeks without the occurrence of any noticeable change in the condition of the parasites. This fact and the manifest immaturity of all the parasites examined makes me believe that the leech is an intermediate host and that the nematode probably attains maturity after passing from the body of the leech into that of another host, perhaps some fish, which feeds upon the leech. How the nematode gets into the body of the leech is likewise unknown, probably from the body of some snail or other small pond animal on which the leech feeds.

The supposed *trematode* parasite I have observed but once, in November, 1899, when three individuals were observed encysted in a single G. stagnalis. Unfortunately they with their host died in captivity before I had an opportunity to study them carefully. They lay imbedded in the deeper muscle layers of their host's body, toward its anterior end, each enclosed in a delicate rounded cyst. A single ventral sucker was observed in the parasite and this seemed to lie a little nearer one end of the body. Toward the opposite end, a dark granular substance was observed in the interior of the body, probably in the digestive tube. My study of the parasite, was so incomplete that I should not feel warranted in asserting the absence of a second sucker more nearly terminal in position than the one observed. No measurements of the cysts were made, but I should estimate their diameter roughly at 0.50–0.75 mm.

About half of the individuals of G. elongata which have come under my observation contain a *gregarine* which appears to be identical with that described by Bolsius ('96) as occurring in G. complanata (Clepsine sexoculata). I have not, however, made a sufficiently careful study of it to enable me to add anything to his account. I find the parasite attached *always to the wall of the stomach diverticula* (Figure 27, *ga.*), never in crop or intestine.

A majority of the individuals of G. fusca collected by me contain *sporozoa* in an encysted condition. These parasites are quite common also in the body of G. heteroclita and that of G. elegans, and I have found them in a single individual of G. stagnalis.

Whether or not they represent another stage of the gregarine found in G. elongata, I am unable to say. As already indicated, I have observed them only in stages of encystment, more or less advanced. One finds the heavily staining sporocyst in whole preparations of its host, usually near the margin of the body, imbedded in the deeper-lying muscle layers (longitudinal and dorso-ventral). The sporocysts which I have observed were spherical in form; the largest ones examined were about 0.13 mm. in diameter and were protected by a thick, dense wall. I have not yet been able to obtain sporocysts containing fully formed spores. Data, accordingly, are wanting for a full description of this parasite, as well as of the others mentioned, and only a portion of its life history is known. Nevertheless I insert this notice in the hope that some one else may be able hereafter to make use of my fragmentary observations.

Cambridge, Mass., June, 1900.

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EXPLANATION OF PLATES.

All figures were drawn with the aid of Abbé's camera lucida, unless otherwise stated in the explanation of figures.

Arabic numerals in the figures designate rings, which, except in the case of Figures 23 and 27, Plate 6, are numbered from the extreme anterior end of the body backward; Roman numerals designate somites numbered in the same manner.

ABBREVIATIONS.

act.	Acetabulum (posterior sucker).	*oc.*	Eye.
an.	Anus.	*œ.*	Œsophagus.
cb.	Brain.	*or.*	Mouth.
dt. ej.	Ejaculatory duct.	*po.* ♂	Male genital pore.
ga.	Stomach.	*po.* ♀	Female genital pore.
gl. d.	Dorsal gland.	*pr'b.*	Proboscis.
gl. sal.	Salivary glands.	*sac. phy.*	Pharyngeal sac.
in.	Intestine.	*suc. or.*	Oral sucker.
i'glv.	Crop.	*te.*	Testis.
lac. marg.	Marginal lacuna.	*va. df.*	Vas deferens.
nph'po.	Nephropore.	*va. ef.*	Vas efferens.
oa.	Ovary.	*vs. sem.*	Seminal vesicle.

PLATE 1.

Fig. 1. *G. stagnalis.* Entire digestive tract shown; somite limits indicated by transverse lines, rings not represented. From an entire preparation. × about 16.

Fig. 2. *G. parasitica.* Parasagittal section of head end of a small individual taken from a turtle (probably Chelopus insculptus Le Conte) bought in a Philadelphia market. Only one (the largest) of the three closely associated pairs of eyes appear in the section.

Fig. 3. *G. stagnalis.* Ventral view of head end, showing mouth, oral sucker, and the marginal sensillæ and annulation of somites I.–VI. From an entire preparation. × 83.

Fig. 3 *a*. *G. parasitica.* Dorsal view of brain.

Fig. 3 *b*. *G. parasitica.* Ventral view of anterior part of a small individual obtained from the same source as that shown in Figure 2. From an entire preparation.

PLATE 1.

PLATE 2.

Fig. 4. *G. stagnalis.* Diagram showing annulation, central nervous system, reproductive organs (male in left, female in right half of figure), nephropores, etc. The outline of the body was drawn from a whole preparation (× about 16); everything else is diagrammatic, representing the *average* form and position of organs as determined by examination and comparison of several individuals.

Fig. 5. Brain of *G. elegans,* ventral view. From an entire preparation. × 52.

Fig. 6. *G. parasitica.* Dorsal view of a young individual from Havana, Illinois, partially extended. × about 10. The starlike structures indicate papillæ; not all of those shown were observed in the individual figured, some being supplied from the study of larger individuals in which the papillæ are more conspicuous.

PLATE 2.

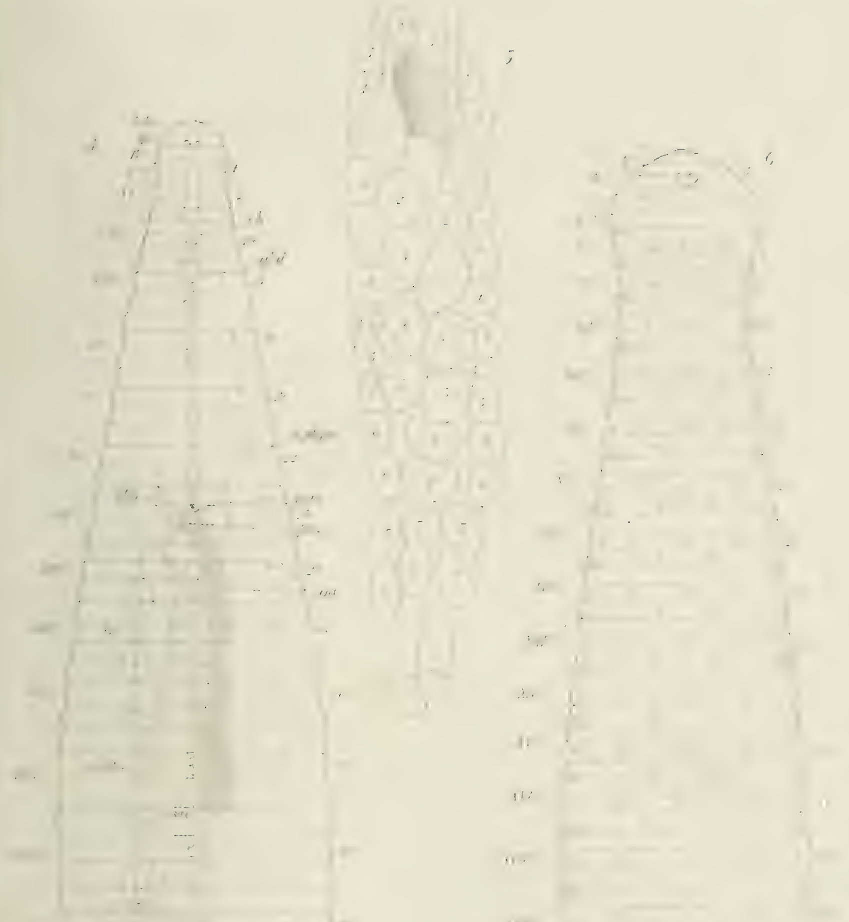


PLATE 3.

Fig. 7. *G. stagnalis.* Parasagittal section of anterior part of body. × 96.

Fig. 8. *G. stagnalis.* Brain viewed from left side. Reconstructed from sections. × 208. Roman numerals designate segmental nerves; Arabic numerals, the ganglionic capsules which supply nerve fibres to same.

Fig. 9. *G. stagnalis.* Posterior part of ventral ganglionic chain, dorsal view, reconstructed from frontal sections. Arabic numerals designate ventral ganglionic capsules; Roman numerals, metameric nerve bundles. × 170.

Fig. 10. *G. stagnalis.* Diagram showing the arrangement of ganglionic capsules on the ventral surface of brain.

Fig. 11. *G. elegans.* Dorsal view of brain.

Fig. 12. *G. stagnalis.* Dorsal view of anterior part of brain. From frontal sections combined. × 167.

PLATE 3.

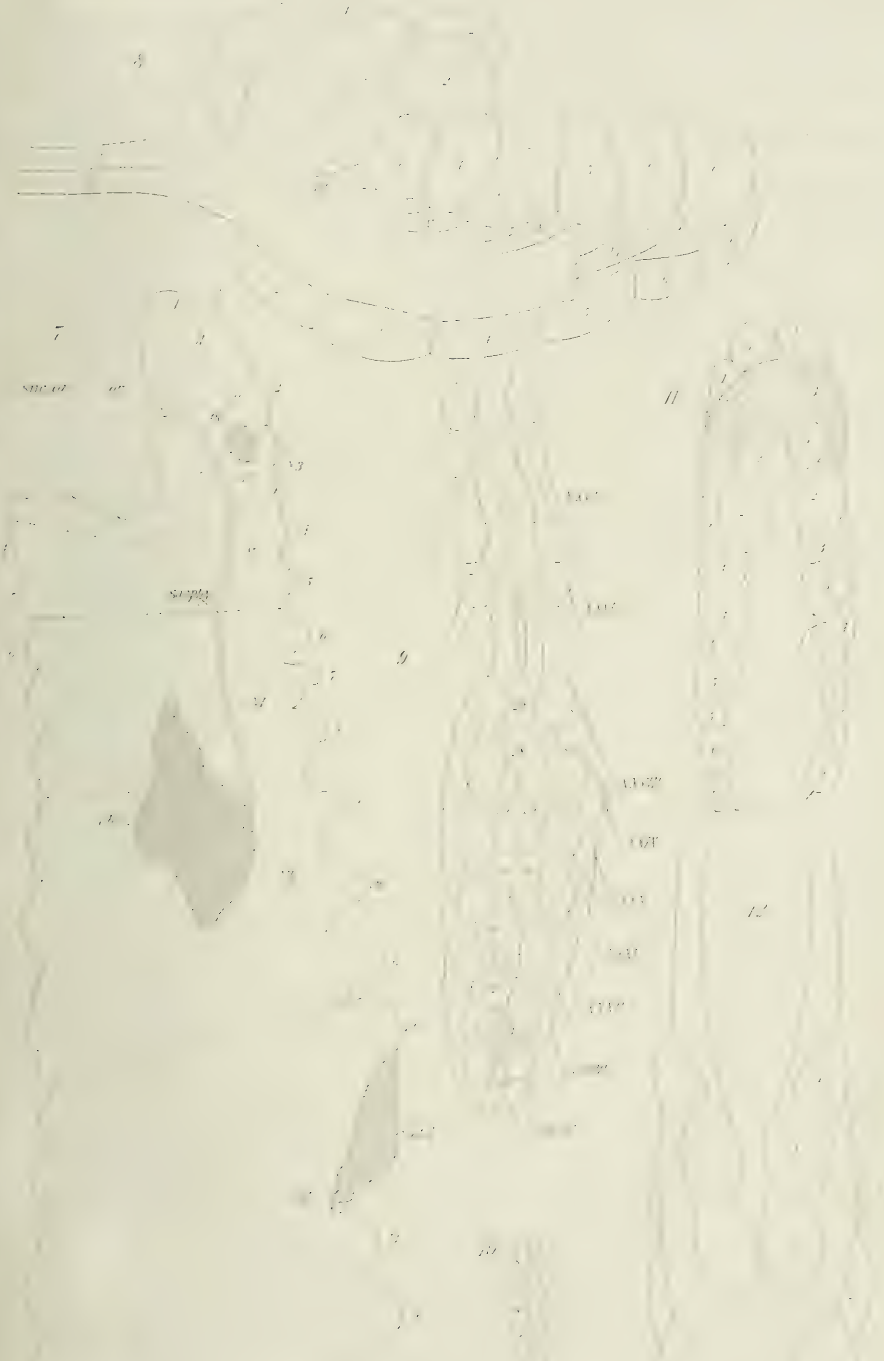


PLATE 4.

G. fusca.

Fig. 13. Dorsal view of a small individual. For clearness furrows between annuli are represented only at the margin of the body, except where they mark somite boundaries. Testes are shown only in the right half of the figure, salivary glands only in the left half. From an entire preparation. × about 34.

Fig. 14. Parasagittal section of head end. × 52.

Fig. 15. Head end of young individual viewed from left side. From an entire preparation. × 83.

Fig. 16. Head end of individual shown in Figure 13. Dorsal view. × 83.

Fig. 17. Group of reserve-food cells from one of the segmental clear spots marking the sensory annuli. From a living animal. × 365.

Fig. 18. Ventral view of brain. From an entire preparation. × 208.

PLATE 6.

PLATE 5.

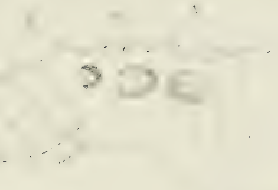
G. heteroclita.

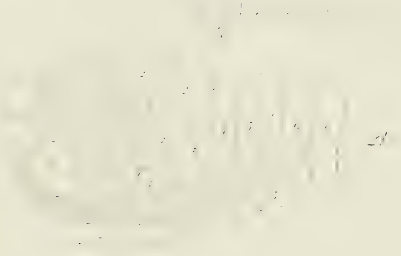
Fig. 19. Dorsal view of a rather small individual. For clearness furrows between annuli are shown only at the margin of the body, except where they mark somite boundaries. Salivary glands are shown only in the right half of the figure, testes only in the left half. From an entire preparation. × 62.

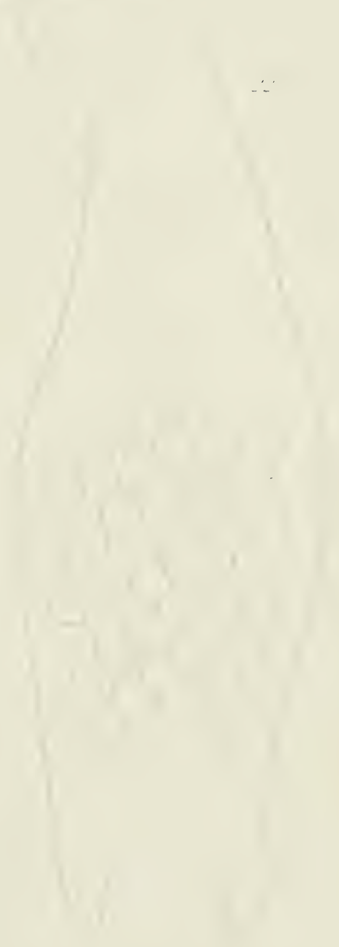
Fig. 20. Combination of two or three successive parasagittal sections of head end. × 83.

Fig. 21. Brain viewed from the left side. From several sections combined.

Fig. 22. Ventral view of a living animal bearing eggs. × about 13.







E. Meisel lith. Berlin

PLATE 6.

G. elongata.

All figures of this plate were drawn from whole preparations. *Annuli in Figures* 23 *and* 27 *are numbered from the posterior margin of the oral sucker backward.*

Fig. 23.	Head end viewed from right side.
Fig. 24.	Posterior end of body viewed from right side.
Fig. 25.	Brain, ventral view.
Fig. 26.	Brain viewed from right side.
Fig. 27.	Ventral view of entire animal partially contracted. In somites vii.–xxii. furrows between annuli are shown only at the margin of the body, except where they mark somite boundaries.

PLATE 7.

G. elegans.

Fig. 28. Dorsal view of a young individual. In somites VI.–XXV. furrows between annuli are shown only at the margin of the body, except where they mark somite boundaries. Reproductive organs and salivary glands drawn from other, older individuals; salivary gland cells a little too small. From an entire preparation.

Fig. 29. Parasagittal section of head end.

Fig. 30. Head end, dorsal view. From an entire preparation. × about 50.

Fig. 31. The same, ventral view.

PLATE 8.

Fig. 32. *G. parasitica, var. plana.* Dorsal view of head end of an individual from Havana, Illinois, in which the division between rings 2 and 3 was not evident. Stippling shows position of yellow pigment in a median vitta and (on left side) in metameric marginal spots. From an alcoholic specimen. × 41.

Fig. 33. *G. parasitica, var. rugosa.* Dorsal view of head end of an individual from Cambridge, Mass., showing the usual annulation of somites i.–iii. From an alcoholic specimen. Enlarged.

Fig. 34. *G. stagnalis.* Dorsal view of posterior end of body. Enlarged.

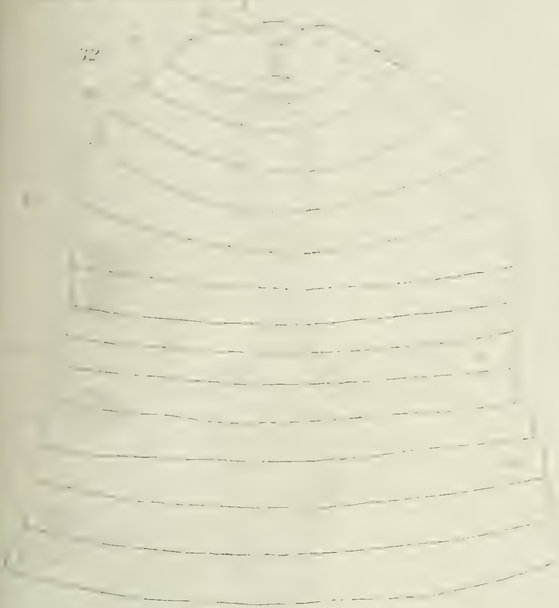
Fig. 35. *G. heteroclita.* Dorsal view of head end of a living animal, showing most common position of eyes. Enlarged.

Fig. 36. A dorsal view of the head end of the individual represented in Figure 38. The anterior ring of somite vi. is seen to contain traces of a transverse pigment line. Drawn from the living animal. Enlarged.

Fig. 37. *G. parasitica, var. plana.* Dorsal view of posterior end of body of the individual shown in Figure 32. Marginal light spots indicated by stippling. × 24.

Fig. 38. *G. heteroclita.* Dorsal view of a living animal, showing the general form of the body at rest, and the color pattern sometimes present on the dorsal surface. The rings are not indicated, but the numerals are placed opposite and serve to designate those rings in which the pigment is found (the anterior rings of their respective somites). Enlarged.

32.



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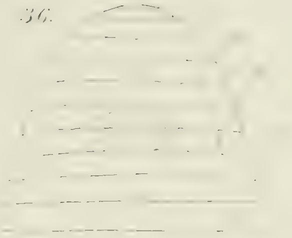

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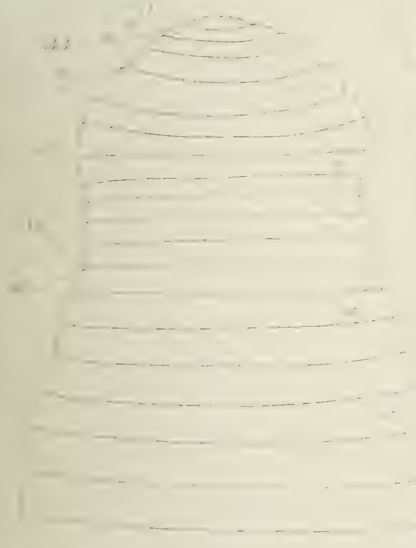

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Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
Vol. XXXVI. No. 3.

FOSSIL LEPIDOSTEIDS FROM THE GREEN RIVER SHALES OF WYOMING.

By C. R. Eastman.

With Two Plates.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
August, 1900.

No. 3. — *Fossil Lepidosteids from the Green River Shales of Wyoming.* By C. R. Eastman.

The Eocene Green River Shales of Wyoming have long been noted for their numerous and beautifully preserved fossil fishes, and large collections have found their way to various American and foreign museums. During the summer of 1899 the Museum of Comparative Zoölogy purchased of Mr. D. C. Haddenham, a local collector at Fossil, Wyoming, two remarkable specimens from the fishbearing shales near that well-known locality. One of these is a gigantic Lepidosteid, of which only detached fragments have hitherto been known; the other is a nearly perfect skeleton of a gallinaceous bird. Both specimens are unique in their way, and possess considerable scientific as well as intrinsic value. The news of their discovery was first communicated by Professor Wilbur C. Knight, of Laramie, Wyoming, who made a special visit to Fossil for the purpose of examining the remains, and whose favorable report induced their acquisition.

A brief account of the two specimens, accompanied by a photo-reproduction of the bird, was prepared soon after their arrival in Cambridge, and published in the Geological Magazine for February, 1900. Later it developed through correspondence with Mr. F. A. Lucas, Curator of Comparative Anatomy in the United States National Museum, that this Museum had also obtained during the past summer a large cranium of Lepidosteus from the same horizon and locality. Another nearly complete fossil gar which had been exhibited at the World's Fair in 1893 was reported, and Mr. Lucas was fortunate enough to ascertain its whereabouts and finally to obtain it too for the national collection. Descriptions of these three specimens are given in the present paper, and it is to be observed that these are the only noteworthy remains of Lepidosteus that have yet been found in the American Eocene.

The discovery of fossil gars in the Tertiary of this country was first reported by O. C. Marsh (Proc. Acad. Nat. Sci. Phil., 1871, p. 105). He named two species, *Lepidosteus glaber* and *L. whitneyi*, both from the Eocene of Wyoming; but as no descriptions were given beyond the bare statement that the first "has unusually short vertebræ" and the other has them "proportionally longer," these names were deservedly rejected by Cope as *nomina nuda*.

A number of species have since been described by Leidy and Cope, all founded on more or less fragmentary remains such as detached vertebræ, scales, and cranial fragments. The only one represented by a tolerably complete individual is *L. cuneatus* (Cope) from the Miocene of Central Utah, the type of which is about 30 cm. in length. The remainder are characterized by A. S. Woodward in his Catalogue of Fossil Fishes as "all too imperfect for specific, and the majority even for generic determination." For instance, Leidy's *L. notabilis* is founded on a single vertebral centrum, which may or may not be identical with those described by him as *L. atrox*. The type species of "Clastes," *L. cycliferus* (Cope), is founded on a few cranial bones and scales. There is still less reason for regarding "Pneumatosteus" as a distinct genus, the type of *P. nahunticus* Cope being an opisthocœlous vertebral centrum from the Miocene of North Carolina.

It is obvious from the foregoing that all the specific titles applied to fossil gars from this country, with the single exception of *L. cuneatus*, have had up to the present time only a provisional significance. They have stood at best for imperfectly definable fragments, which were in some cases with difficulty distinguished from one another. Thanks to the newly discovered material, however, we know what the complete fish in at least two species besides *L. cuneatus* was like, and the cranial osteology of the larger one is as readily decipherable as that of a recent gar. In all, four species are recognized from the American Eocene, and two from the Miocene, as follows: —

L. atrox Leidy (= *L. anax* Cope). Middle Eocene; Wyoming.
L. simplex Leidy. Middle Eocene; Wyoming.
L. notabilis Leidy. Eocene; Wyoming.
L. (*Clastes*) *cycliferus* (Cope). Eocene; Wyoming.
L. (*Clastes*) *cuneatus* (Cope). Miocene; Central Utah.
L. (*Pneumatosteus*) *nahunticus* (Cope). Miocene; North Carolina.

Turning to the European representatives of this family, we find only seven or eight species, likewise founded on fragmentary remains such as scales, vertebræ, cranial fragments, etc., but nowhere a complete skeleton. The range is from Lower Eocene to Lower Miocene, and the distribution sparse in various localities of England, France, and Germany. With pardonable pride, therefore, we may point out that the specimen immediately to be described is at once the largest and most perfect fossil gar ever brought to light. It lacks any positively archaic features and bears close resemblance to living forms. It is obviously the direct progenitor of the modern Alligator gar, *L. tristœchus* (Bloch and Schneider), and compares with it very favorably both in size and general characters. But if we inquire into the more remote or pre-Eocene history of Lepidosteids, palæontology gives us no answer. They blossom forth suddenly and fully differentiated at the dawn of the Tertiary without the least clue to their ancestry, unheralded and unaccompanied by any intermediate forms; and they have remained essentially unchanged ever since.

Lepidosteus atrox Leidy.

Plate 1, Fig. 2; Plate 2.

1873. *Lepidosteus atrox* Leidy, Proc. Acad. Nat. Sci. Phil., p. 73.
1873. *Lepidosteus atrox* Leidy, Rept. U. S. Geol. Surv. Territ., Vol. I., p. 189, Plate XXXII, Figs. 14, 15. (Vertebræ.)
1873. *Clastes atrox* Cope, Ann. Rept. U. S. Geol. Surv. Territ., 1872, p 634.
1873. *Clastes anax* Cope, *loc. cit.*, p. 633.
1884. *Clastes atrox* Cope, Rept. U. S. Geol. Surv. Territ., Vol. III, p. 54, Plate II, Figs. 1–24.
1884. *Clastes anax* Cope, *loc. cit.*, p. 53, Plate II, Figs. 50–52. (Cranial bones.)
1900. *Lepidosteus atrox* Eastman, Geol. Mag. [4], Vol. VII, p. 57

Definition. — A large species, equalling the recent Alligator gar in size and resembling it in general characters. Head contained about four times in total length; snout short and broad. External bones very heavy, ornamented with ramifying lines of ganoine tubercles which become consolidated into more or less radiating ridges on the operculum and suboperculum. Jaws with an outer series of numerous small teeth followed by a single series of large, regularly spaced, conical, striated teeth implanted vertically in a rather deep and narrow furrow. Dorsal and anal fins remote, nearly opposed; caudal only slightly convex; pelvic situated about midway between the pectorals and anal. Dorsal fin-rays 8, caudal 12, anal 8, pelvic 6. Fulcra biserial and prominent on all fins. Scales very robust, in 18–20 longitudinal series, and between 50 and 60 oblique transverse series counting along the lateral line. Surface of scales smooth or with feeble ornamentation, consisting of pittings and papillæ; posterior margin fimbriate, especially so in scales of abdominal region. Post-clavicular scales prominently sculptured.

Preservation. — Except for the head, the specimen is very well preserved, and the fin-rays remarkably so. Two thirds of the fish, including the head, lies squarely on the ventral surface, but in the abdominal region the body is twisted, so that the right lateral aspect is exposed from the tip of the tail to a point midway between the anal and pelvic fins. The squamation is somewhat disturbed anteriorly, scarcely at all so posterior to the line of flexure. All the fins with the exception of the pectorals are beautifully preserved, but both pectorals are very defective. Notwithstanding the thickness of its separate plates, the cranial box yielded to pressure of the overlying matrix, and became irregularly flattened prior to fossilization. Most of the external head-bones are displaced, and the only ones escaping serious injury are the opercular apparatus and jaws of the right-hand side. The cranium, therefore, is in a very unsatisfactory condition for study, and it is fortunate our knowledge of its osteology is supplemented by a second specimen, which is described below.

Cranium. — Turning our attention first to the right-hand side of the head, we find that the operculum, suboperculum, interoperculum, preorbitals, maxillary and mandibular ramus all occupy their normal position with respect to one another, being simply flattened out, not displaced. The opercular plates have practically the same configuration and arrangement as in recent species, but are many times more massive, thus harmonizing with the powerful armoring of the trunk. The postero-inferior angle of the interoperculum is developed into a stout, blunt process overlapping the suboperculum. The latter plate, together with the operculum, has a slightly different ornamentation from the remaining bones of the head, in that the ganoine tubercles are fused into more or less continuous and radiating ridges. On the jaws and bones forming the roof of the head the tubercular ridges are ramifying and irregularly confluent.

The maxillary is preserved in its entirety and measures 19 cm. in length. Anteriorly it shows a fontanelle as in recent forms, but traces of its segmentation are now nearly obliterated. In the Washington cranium described by Mr. Lucas the segments are very distinct, and are seven in number. (See *infra*, p. 73). As the oral aspect of the maxillary is not exposed, nothing can be affirmed of its dentition. Considering its extreme narrowness, however, and the fact that only a single dental groove is opposed to it in the lower jaw, it is improbable that more than one series of large teeth was present In this character a noteworthy difference is to be observed between the species under consideration and the recent *L. tristœchus* (= *L. viridis Gthr.*), with which it stands otherwise in close agreement; and incidentally it proves the artificial nature of Rafinesque's subgenus Atractosteus. For if we emend the definition of the latter so as to include its nearest allied fossil species, no characters are left by which it can be distinguished from Lepidosteus *s. str.* Hence it seems best to discard altogether the subgeneric terms Atractosteus and Cylindrosteus.[1]

The mandibular ramus is 25 cm. long and composed of the usual parts, dentary, angular, and coronoid. Immediately behind the last-named element are two circumorbital plates, but all the remaining circumorbitals and suborbitals are crushed into a confused mass. The outer rim of the dentary is set with a series of numerous minute teeth, next to which is placed a single series of large conical teeth implanted vertically in a narrow and moderately deep longitudinal groove. There are nine of these teeth spaced at regular intervals from the symphysis to about the middle of the lower jaw. They are of nearly uniform size, about 2 cm. in height, and vertically striated. Coronal cross-sections show the complicated structure of dentine characteristic of the genus. The symphysial teeth are directed forwards at a slight angle. The symphyses of both rami lie contiguous to one another in the limestone, but by far the greater portion of the left mandibular ramus and whole of the left maxillary are concealed by overlying bones.

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[1] According to Jordan and Evermann (Bull. 47, U. S. Nat. Mus., pt. 1, p. 109), "The name *Litholepis*, Rafinesque, applied by him to a gigantic gar, *Litholepis adamantinus*, the 'Devil-jack Diamond Fish,' is based on a drawing by Audubon, not intended by Audubon to represent any possible fish."

Next above the right maxillary lie a pair of long and narrow, deeply channelled or folded elements, which presumably represent the palatines; and adjacent to these are the median series of bones belonging to the cranial roof, which are now laterally displaced and very considerably injured. The oblique sutures between the frontals and ethmonasals are well shown, and also the sutures along the median line of the head. Premaxillaries and nasals are not preserved, and most of the bones belonging to the otic and occipital region are either missing or crushed beyond recognition. For this reason the length of the head in the median line cannot be accurately determined, although a conservative estimate would place it at about 40 cm. The distance in a straight line from the symphysis of the lower jaw to the posterior margin of the operculum is 45 cm. The right and left clavicle are partially visible behind the head, but are in nowise remarkable either in size or configuration.

Fins. — Very little remains of either of the pectorals, but all the remaining fins are beautifully preserved. The dorsal and anal are triangular, broad-based, and relatively high (20–22 cm.), with eight dermal rays each. These fins are very remote, and nearly opposed to each other. The caudal has a length of 24 cm., is composed of twelve finely articulated long rays and a lesser number of short rays which differ from the rest in being uniserially articulated throughout their length. Prominent biserial fulcra fringe the dorsal and ventral margins of the caudal and front margins of the remaining fins. The extreme tip of the tail is not preserved, but it was apparently very slightly rounded. The pelvic fins are situated about midway between the pectorals and anal, and resemble the latter in form and size.

The long proximal joints of each dermal ray in all the fins consist of two halves, or right and left portions, rather loosely united along the axial plane, and consequently subject to displacement. These proximal pieces correspond in number to the interneurals, which likewise have suffered some displacement in the dorsal and pelvic fins. Immediately after the proximal joint the rays in all fins become biserially articulated, and after a short interval become further bifurcated, much like the arms of crinoids. It will be seen from the following table that little variation in the radial formula exists amongst the various living and fossil species: —

SPECIES.	RADIAL FORMULÆ.				SCALES OF LATERAL LINE.
L. atrox Leidy	D. 8;	C. 12;	A. 8;	P. 6	50–60
L. simplex Leidy	D. 7;	C. 12;	A. 7 +	?	*circa* 45
L. tristœchus (Bl. and Sch.)	D. 7–8;	C. 12;	A. 8;	P. 6.	60
L. tropicus Gill	D. 8;	C. 12;	A. 8;	P. 6.	52–54
L. platystomus Raf.	D. 8;	C. 12;	A. 8;	P. 6	56
L. osseus (Linn.)	D. 8;	C. 12;	A. 7–9;	P. 6.	62

Scales.—The body armoring is excessively heavy, being on a par with that of the head, and recalling the powerful dermal defences of *Lepidotus maximus* from the Upper Jura. In fact, these two species probably have the strongest scaly coating of all fossil ganoids. Owing to flexure of the body in the present specimen, with consequent disturbance of the squamation anteriorly, it is difficult to count the longitudinal or even transverse scale-series with accuracy. There are no conspicuously marked scales along the dorsal ridge by which the median line of the back can be determined; but making all due allowance for displacement, the number of longitudinal series in the middle of the body may be set down at between 18 and 20, and of transverse oblique series counting along the lateral line at between 50 and 60. A very large anal scale marks the position of the vent. The exposed surface of most of the scales lying between the tail and middle of the body is smooth, but the posterior margin is strongly fimbriate. Some of the scales lying in advance of the pelvic fins are smooth, but the majority have their central portion ornamented with punctæ, pittings, or channellings, and interspersed with these are occasional papillæ. The lateral line in the present specimen is inconspicuously marked. To give enlarged figures of separate scales is hardly considered worth while, owing to the extensive series illustrated by Leidy and Cope. Those figured by Cope (Rept. U. S. Geol. Surv. Territ., Vol. III. Plate II, Figures 8, 10–12) show the typical ornamentation as well as any, and Figures 47 and 48 show the highly sculptured postclavicular plates.

Vertebræ. — The vertebral column is traceable for the greater portion of its length, although it protrudes only at intervals through the mass of scales so as to exhibit the individual centra. For views of detached vertebræ reference must be had to the works of Leidy and Cope already cited. Stout displaced neural and hæmal spines are visible in places along the extent of the vertebral column, and in some places ribs are to be distinguished.

Coprolite. — Accompanying the specimen is a cylindrical coprolite 13.5 cm. long and 5.5 cm. in diameter, which is stated by the collector to have been found in close proximity to the fish. That it is of piscine origin admits of no doubt, and it could hardly have been voided by a smaller species than that under consideration. Its outer surface is marked with a few irregularly spiral folds, but is otherwise smooth. No large hard particles are to be distinguished, and the whole mass bears evidence of very thorough digestion.

Regarding the fine head of *Lepidosteus atrox* (Plate 2) procured by Mr. Charles Schuchert for the United States National Museum while collecting in Wyoming last summer, Mr. Lucas writes: —

"The specimen (Cat. No. 4755) consists of a little more than the anterior half of an individual of about the same size as that belonging to the Museum of Comparative Zoölogy at Cambridge. It lies upon the ventral surface, and while the body has of course been flattened, the cranium has suffered but little from compression, and is almost as favorable for study as a fresh gar would be.

"The general form of the cranium is intermediate between that of *Lepidosteus osseus* and *L. tristœchus*, the muzzle being slightly wider than in the first-named and narrower than in the latter, so that there is no such obvious notch towards the anterior part of the ethmonasals as appears in *L. tristœchus*. At the same time the back of the cranium is proportionately wider in the Eocene than in the living species, the result being that the skull of *L. atrox* tapers somewhat abruptly from behind forward.

"The right vomer is turned outwards exposing its anterior end, and a fracture across the muzzle brings to view a section of the palatines; from these exposures it is possible to state that both vomers and palatines are dentigerous, while in the lower jaw teeth are visible on the dentary. There is no apparent difference between the dentition of *L. tristœchus* and *L. atrox* save that in the present specimen none of the teeth are so large as in the living species. The Cambridge example, however, shows this to be an individual peculiarity. Two nasal plates are present on either side as in existing gars, and the maxillary segments are seven in number, or one more than in the two examples of the Alligator gar available for comparison. The ethmonasals, especially the external sculptured parts, are, as previously noted, narrower in *L. atrox* than in *L. tristœchus*. The frontals are much the same in the two species, but the parietals and squamosals are a little shorter and wider in the fossil than in the living gar. The circumorbitals are displaced and few of them visible, but such as can be seen are notably thick. The same remark applies to the operculum and suboperculum, for although of practically the same size as in *L. tristœchus*, they are decidedly thicker. The cranial bones are also heavy, and their sculpturing while well defined is a trifle finer and decidedly more granular."

PRINCIPAL MEASUREMENTS OF THE WASHINGTON CRANIUM (*cf.* Plate 2).

Length from extreme tip of nasals to end of supratemporals	34.2 cm.
Length of maxillary	15.6
Length of exposed portion of ethmonasal along suture	12.7
Length of frontals along median suture	13.7
Length of parietals along median suture	4.6
Width across anterior part of ethmonasal	4.6
Width across exposed portion of ethmonasal	2.2
Maximum width across anterior portion of both frontals	5.
Maximum width across posterior portion of both frontals, at junction with squamosals	9.8
Maximum width between outer borders of right and left squamosals	14.

Lepidosteus simplex Leidy.

Plate 1, Fig. 1.

1873. *Lepidosteus simplex* Leidy, Proc. Acad. Nat. Sci. Phil., p. 73.
1873. *Lepidosteus simplex* Leidy, Rept. U. S. Geol. Surv. Territ., Vol. I., p. 191, Pl. XXXII, Figs. 18, 26, 31–43. (Vertebræ, jaw-fragments, scales.)

For the opportunity of describing this interesting specimen the writer is indebted to Mr. F. A. Lucas, who obtained possession of it in behalf of the United States National Museum after it had passed into oblivion since being exhibited by a private collector at the Chicago World's Fair. It was derived originally at the typical Green River locality in Wyoming, and bears the catalogue number 4754.

The specific determination is based principally on scale characters, the enamel surface of the few detached scales known to Leidy being described by him as "flat, smooth, and highly polished, and exhibits no markings except one or several minute punctæ near the centre." One peculiar scale, which we can now recognize as belonging to the lateral line and oriented in a wrong position in Plate XXXII, Figure 33, of Leidy's Monograph, is described (Rept. U. S. Geol. Surv. Territ., Vol. I, p. 191) as "traversed fore and aft by a canal communicating by a short cleft with the outer surface. The cleft is directed backward, and is protected by an angular elevation of the anterior border." It would appear to be characteristic of this species that scales of the lateral line are traversed by short vertical canals instead of horizontal clefts, and the remaining scales are flat, smooth, and polished with entire edges. Other distinguishing features will be noted presently, and the definition may be emended as follows: —

Definition. — A species attaining a total length of about 65 cm., of which the head forms one fourth. External bones not especially heavy, arranged as in the recent Alligator gar, but with finer and more granular ornamentation; the ganoine tubercles of operculum and suboperculum forming more or less continuous lines, as in *L. atrox*, but those of the interoperculum fused into irregular ridges. Jaws with an outer series of numerous small teeth followed by a single series of larger ones, the latter, however, relatively of much less size than in *L. atrox*. Vomers dentigerous, but no teeth observed on either palatines or parasphenoid. Fins as in *L. atrox*, but relatively weaker, and dorsal and anal more remote. Scales smooth and highly polished, with entire margins and no ornamentation save for occasional minute punctæ near the centre; scales of the lateral line cleft by a short vertical canal. At least 45 oblique transverse scale-series, and 18 to 20 longitudinal ones. Flank-scales of posterior part of the body considerably elongated in an antero-posterior direction.

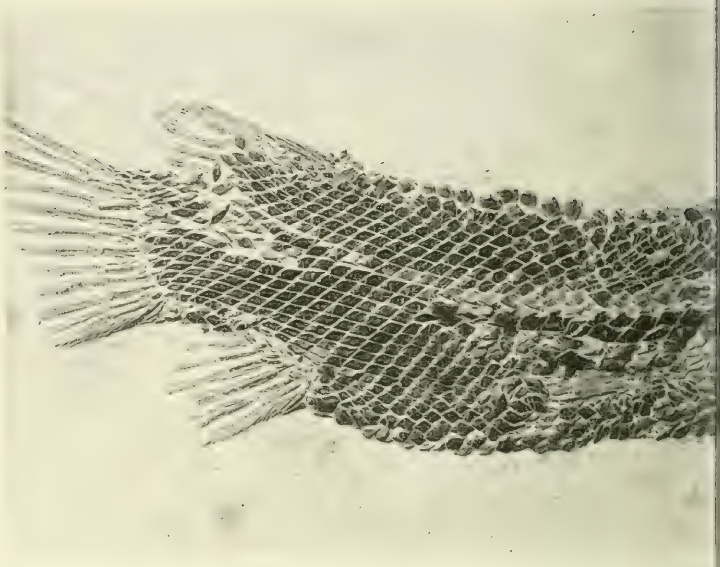
Description. — The total length of the fish when straightened out was probably not far from 64 or 65 cm., or exactly four times the length of the head in the median line. In *L. atrox* and *L. tropicus* the head is also contained four times in the total length, in *L. platystomus* and *L. tristœchus* three and one half, and in *L. osseus* with its specialized snout, but three times. The armoring of the present species is everywhere lighter and simpler than in the massive *L. atrox*, from which it is readily distinguished by its smooth scales with non-fimbriate posterior borders Another peculiarity which is probably of specific importance consists in the marked elongation of the flanked scales beginning with the series in advance of the anal fin and continuing to the tail. Many of the scales thus affected are twice as long as they are deep, which accounts for there being only 15 oblique transverse scale-series between the base of the tail and base of the anal fin, as compared with 21 such series in *L. osseus*, and 23 in *L. tristœchus* and *L. atrox*. Owing to flexure of the body with attendant disruption of the squamation, it is impossible to state accurately the number of oblique rows, but there were at least 45 of them, and possibly 50.

The head appears to have been nearly severed from the body and turned completely over prior to fossilization, thus exposing the visceral surface to view. This was not accomplished without injury or displacement of certain parts, as witnessed by the position of the left palatine, which shows its oral surface adjacent to the right frontal (above in the figure), while the right mandibular ramus, hyoid arches, and interoperculum are transported to the opposite side of the head (below in the figure). Back of the last-named element is seen from visceral aspect the left clavicle, a strong bone similar in all respects to that of recent gars. The interoperculum differs from the corresponding bone in *L. atrox* in wanting a postero-inferior process, and it is relatively much lighter as well as somewhat smaller. Neither of the maxillæ are preserved, and but one of the mandibular rami ; this, the right-hand one, is turned downward so as to conceal most of the teeth, but the articular facets are well shown, and appear exactly as in *L. tristœchus*. Little more can be said of the cranial bones, owing to their confused position and the fact that none of them differ in any appreciable respect from those of recent species.

Of the vertebral column fourteen centra lying in natural order are visible back of the head, their length increasing rapidly from 0.55 cm., beginning with the first, to 0.85 cm. The fins are relatively weaker than in *L. atrox*, especially the caudal, which has fewer short rays , and the dorsal and anal are more remote. The radial formula is as follows : D. 7 (–8?) ; C. 12; A. 7 (–8?).

TABLE OF MEASUREMENTS.

Length of mandibular ramus	10 + cm.
Length of interoperculum	5.2
Length of hypohyal	0.8
Length of ceratohyal	2.5
Length of epihyal	1.0
Height of clavicle	6.2
Height of caudal pedicle	6.0
Width of basioccipital concavity	1.2
Distance from basioccipital concavity to vomer	16.0



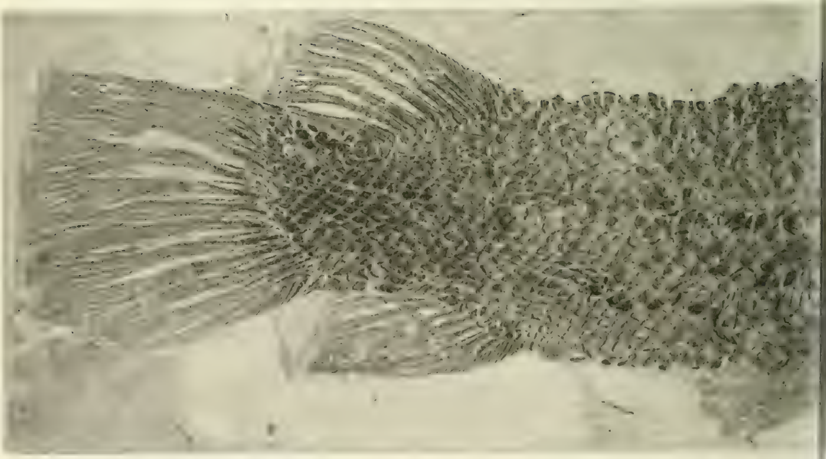
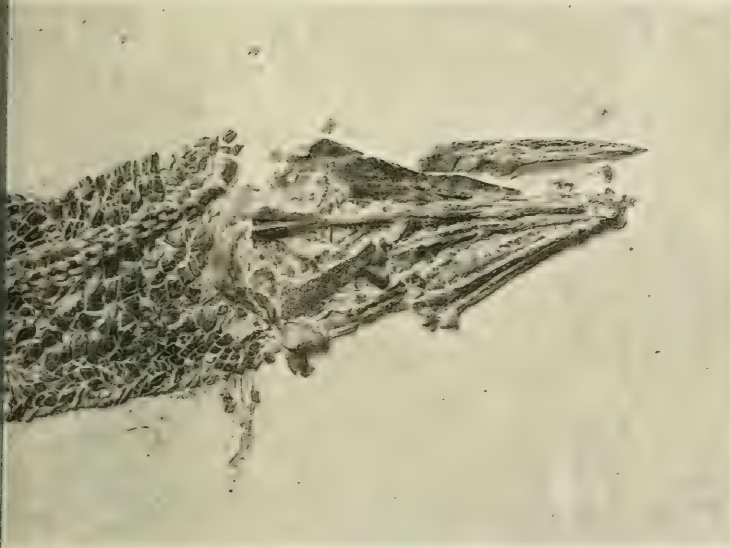
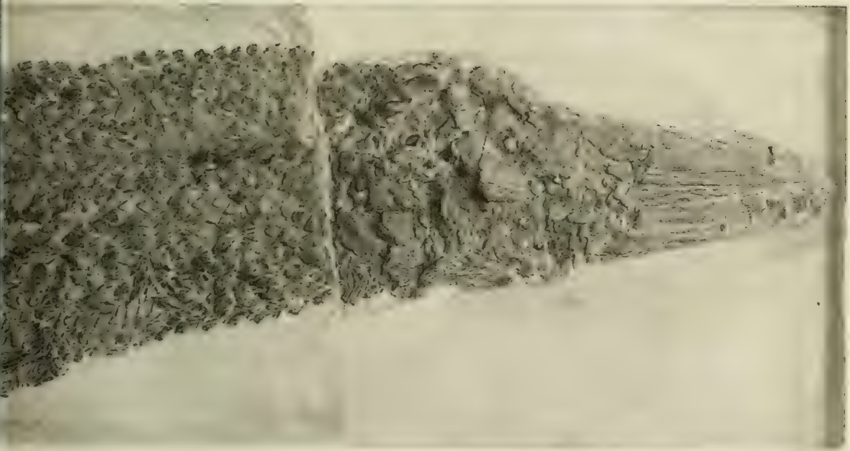


PLATE I.





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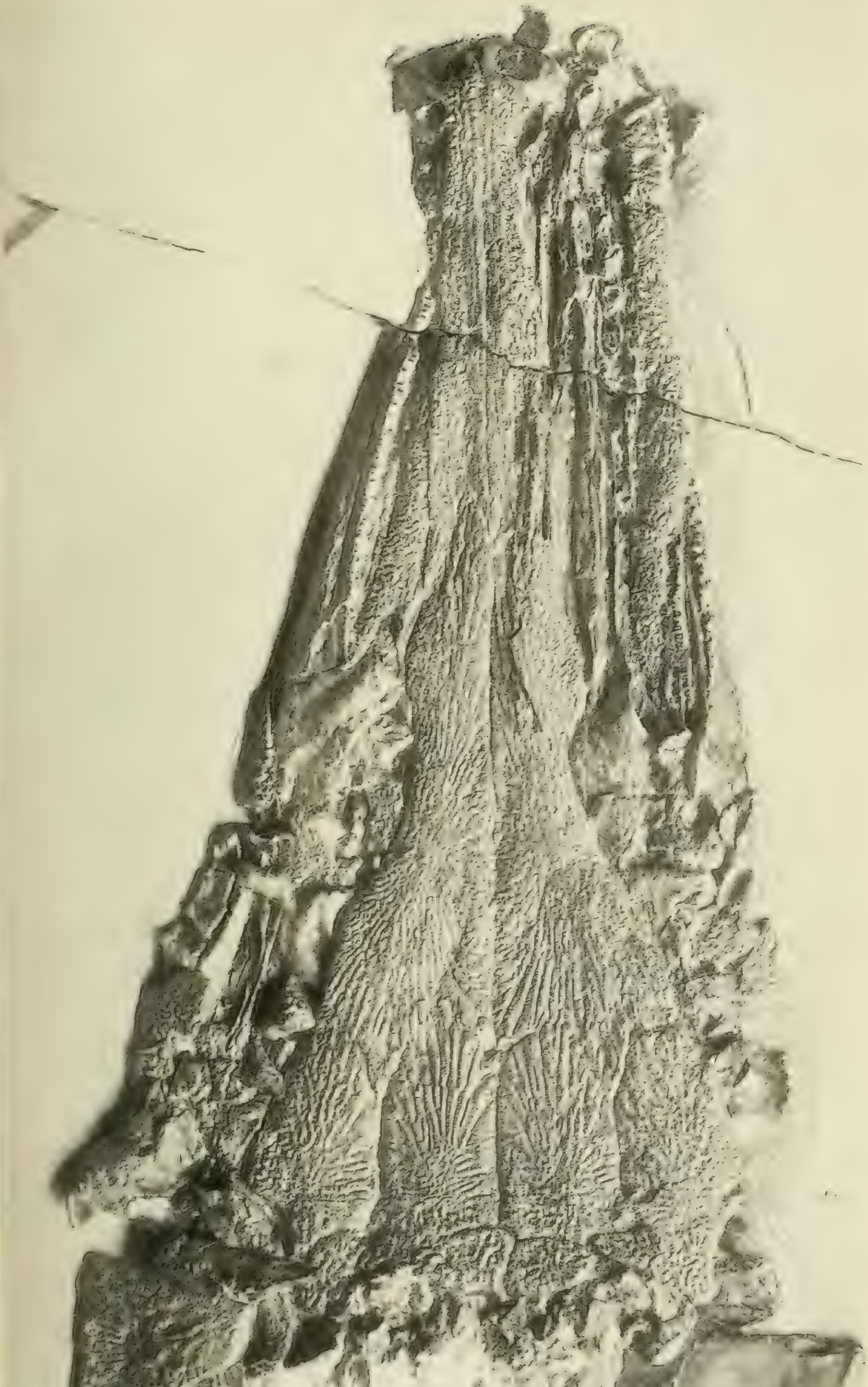

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CHARACTERS AND RELATIONS OF GALLINULOIDES, A FOSSIL GALLINACEOUS BIRD FROM THE GREEN RIVER SHALES OF WYOMING.

BY FREDERIC A. LUCAS.

WITH ONE PLATE.

CAMBRIDGE, MASS., U. S. A.:
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No. 4. — *Characters and Relations of Gallinuloides wyomingensis Eastman, a Fossil Gallinaceous Bird from the Green River Shales of Wyoming.* By Frederic A. Lucas.

The specimen upon which the following observations are based was discovered in the Green River Shales (Middle Eocene) of Fossil, Wyoming, during the summer of 1899, and was shortly after procured for the Museum of Comparative Zoölogy at Cambridge, where it is now preserved (Cat. Foss. Birds, No. 1598). Dr. C. R. Eastman briefly described (Geological Magazine, February, 1900) the bird as *Gallinuloides wyomingensis*, and at his solicitation a more detailed investigation of its structure and relations was undertaken, the results of which are herein set forth.

Like the well-known Green River fishes, the specimen is very complete and in a most excellent state of preservation, although a little injured as to skull, vertebræ, and digits through the over-zealous preparation of the collector. There is a thin, dark, unctuous layer lying on the same plane as the skeleton and almost confluent with the thinner bones, so much so that in developing the finer points it was at times difficult to shun the temptation to carve out a character that might readily be imagined to exist. This layer obscures the ribs, which are scattered, as well as other portions of the skeleton. While, however, many structural details cannot be made out, the general characters are so distinct and the affinities of the bird so apparent that these defects are of comparatively small importance.

The Green River bird was of about the size of a Ruffed Grouse, but stood somewhat higher on its legs. Its galliform nature is obvious at a glance, the most apparent peculiarities being the length of the legs and the depth and the anterior extent of the sternal keel. The majority of its structural resemblances are with the curassows and with the genus Ortalis amongst those birds, but while according to Huxley's definition it indisputably falls in the Peristeropodes, there are sufficiently strong characters to exclude it from both the Cracidæ and Megapodiidæ. The bird presents no points of affinity with any of the American grouse, still less with any of the Odontophorinæ.

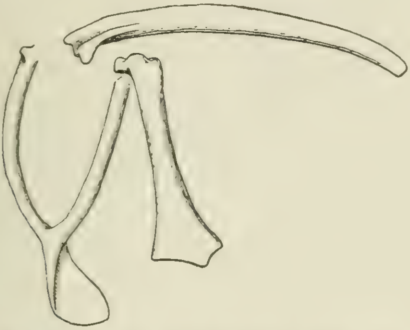
Cracine and Galline are herein used as short equivalents for "peristeropodous" and "alectoropodous," — the latter terms, although expressing the precise meaning needed, being a trifle cumbersome for ordinary use; "galliform" is employed to designate such characters as are shared in common by all members of the Galliformes.

Head. — The beak much resembles that of Ortalis, being moderate in size, stouter than in Crax, Rollulus, and Phasianus; but not so short, stout, and decurved as in Colinus and allied genera. The holorhinal narial opening is also much like that of Ortalis, and the nasal, which has escaped injury, is typically galliform; the superior process can be clearly seen, but the inferior process is covered on its lower part by crushed bone. The lachrymal, or prefrontal, appears to have been well developed, contrasting in this respect with the American grouse (in which the prefrontal is usually quite small), and agreeing with the curassows. The postfrontal process is stout and directed forwards. The mandible is stout and imperforate, and while it has a blunt angular projection, the recurved process so characteristic of the Galliformes is lacking. This is the most notable departure from the galliform structure found in the skeleton.

Vertebræ and Ribs. — Little can be said of the vertebræ save that the vertebral column presents the customary galliform arrangement of a free vertebra in front of the synsacrum preceded by a mass of anchylosed vertebræ, but as to the number of the latter nothing can be affirmed. The cervicals have suffered from the mistaken zeal of the preparator, and but five can be definitely distinguished between what should be the axis and where the column disappears in the flattened bones of the wings. The caudals are mostly lacking, so that, unfortunately, nothing can be learned from them.

Four pairs of ribs are articulated with the sternum, and at least one pair (one is the customary number in the Galliformes) arose from the synsacrum. Several ribs lie over the synsacrum, but there is no reason to suppose that all of them articulated with it. The usual number of ribs among the Galliformes is five on a side; Pavo has six, but the number in the present specimen cannot be made out. There is quite a little space between the first and second costal facets, the succeeding three being crowded together. This is interesting from the fact that it is a feature of modern galline birds, the spacing of the costals being more regular among the curassows.

Shoulder Girdle. — The scapula is not unlike that of Rollulus, being long, narrow, and with parallel borders, as in many of the curassows, or as in Pediocetes. The coracoid resembles that of the Old World pheasants, and especially that of *Phasianus colchius,* more than it does the corresponding bone in any of the curassows. The epicoracoid is a little more angular than is customary among Galliformes, but the epicoracoid of Pediocetes is of much the same pattern, and in this small point the Green River bird makes its nearest approach to some of the American grouse. The precoracoid process appears to be absent, as it is in most Galliformes, although there is a suggestion of this process in Arboriphila. The scapular process is small. The distal end of the coracoid makes a more obtuse angle with the shaft than is usual even in galline birds, but in this respect it is very similar to *Phasianus colchius.*



Scapula, coracoid, and furcula, natural size.

The furcula is unusually short and stout for a gallinaceous bird, exceeding in this respect any species with which it has been compared ; it is U-shaped rather than V-shaped, most nearly resembling Numida in this particular. There is a distinct though slight acrocoracoid process, so that the furcula did not merely rest against the inner side of the coracoid, but articulated with it, thus differing from all existing Galliformes. The scapular ends of the furcula are hidden so that it cannot be positively stated whether or not they reached the scapula. The hypocleidium is large and triangular, contrasting with Crax, which has a spinous hypocleidium, and exceeding Ortalis, in which this process is subtriangular and of moderate size.

The sternum has a manubrium of moderate size, but from the disposition of the bones it is impossible to ascertain whether it is perforate or imperforate. Both the external clefts are quite deep, and the external as well as internal xiphoid process is directed well backward ; both processes are expanded at the free end. In the specimens of curassows available for comparison the external xiphoid is not pedate, but there is a suggestion of this condition in Talegallus. The sternal clefts are typically cracine, there being no approach to the deep internal cleft which makes the external and internal xiphoids of galline birds really branches of one process. The keel of the sternum is produced more anteriorly than in other Galliformes, though nearly approached by Centrocercus. It is to be noted that in this latter form the furcula is unusually long and narrow.

Fore-limb. — The humerus, like the other bones of the wing, is stout and has the deltoid process well developed. The crushing which the bone has undergone prevents its being definitely stated whether or not the humerus was pneumatic, although the probabilities are that it was not. The structure of the wing, in conjunction with that of the sternum, indicates a bird of good powers of flight. The other bones of the wing lie so nearly over one another and are so flattened together that little can be said as to their details, save that the third metacarpal appears to have been much straighter than is usual among gallinaceous birds.

Pelvic Girdle. — As the pelvis lies on its dorsal surface it cannot be stated whether or not it was curved or straight in profile, but in the subequal proportions of the pre- and post-acetabular portions it resembles the curassows, although the conditions are much the same in Meleagris. It is somewhat wider in comparison with its length than in the curassows, the proportions resembling those observed in Thaumalea. There is no tendency toward separation of the ilia and ischia. The ischia do not seem to be bulged out to overhang the pubes as they do in Ortalis, but this feature is so extremely variable in the Galliformes as to have little or no significance. The pubes are long and slender, and as the specimen now lies, they appear parallel with one another throughout their distal halves. In most Galliformes the pubes approach each other distally, sometimes, as in Ortalis and Penelope, being almost in contact. In this respect the Green River specimen departs from the cracine type and approaches such forms as Meleagris and Rollulus, and while it is of course possible that the pubes may have approached each other in the living bird, the intervening space is now so great as to make this seem doubtful. The prepubis is small, the obturator foramen very small, and the ilio-ischiadic space moderate.

Hind-limb. — The femur is so crushed as to obscure its characters. There is no sign of a patella, though this may have been present. The cnemial ridges are slight, and there is the customary osseous tendinal bridge on the anterior face of the distal end of the tibia. The fibula is of the same general proportions as in other Galliformes.

The hypotarsus is very likely only grooved, not perforate; but this is one of the points that cannot be definitely ascertained without injury to the specimen. The number of tarsal tendinal perforations is a character of much importance in birds, for it seems fairly constant within the limits of a given large group and indicates the amount of specialization attained by the members of that group. As all Galliformes examined have a single tendinal perforation, the absence of such a character would indicate that our Eocene bird is of a more primitive type than its modern relatives. The usual tarsal sesamoid shows back of the right tarsal joint. The tarsus is longer in proportion to the tibia than in any other species examined, as is shown by the subjoined table, which gives the length of these bones in a few species: —

SPECIES.	LENGTH OF TIBIA.	LENGTH OF TARSUS.	RATIO.
Gallinuloides wyomingensis	57° mm.	45° mm.	1.27
Penelope superciliaris	115.	82.	1.40
Rollulus roulroul	72.	48.	1.50
Phasianus colchius	112.	72.	1.56
Ortalis maccalli	108.	65.	1.66
Colinus virginianus	53.	30.	1.77

The toes are moderate and slender, of about the same length as those of *Colinus virginianus*, but a little heavier; yet they are not heavy in comparison with the size of the tarsus or the general bulk of the bird.

The following table gives the length of the principal bones in the skeleton, all measurements being made in a straight line: —

PRINCIPAL MEASUREMENTS OF GALLINULOIDES WYOMINGENSIS.

Occipital condyle to tip of bill,	47.° mm.	Xiphoid to anterior end of keel,	59 + mm.
Humerus,	47.	Femur,	41.
Ulna,	49 +	Tibia,	57. +
Metacarpus,	25.	Tarsus,	45.
Scapula,	48.	Basal phalanx of digit I.,	7.5
Coracoid,	29.	do do do II.,	11.
Xiphoid to manubrium,	59. +	do do do III.,	12.
		do do do IV.,	7.5

Relationships. — The various characters of the Green River bird may be summarized as follows: —

Galline Characters. — Pedate end of internal xiphoid process, arrangement of the costal facets, and shape of the distal end of coracoid.

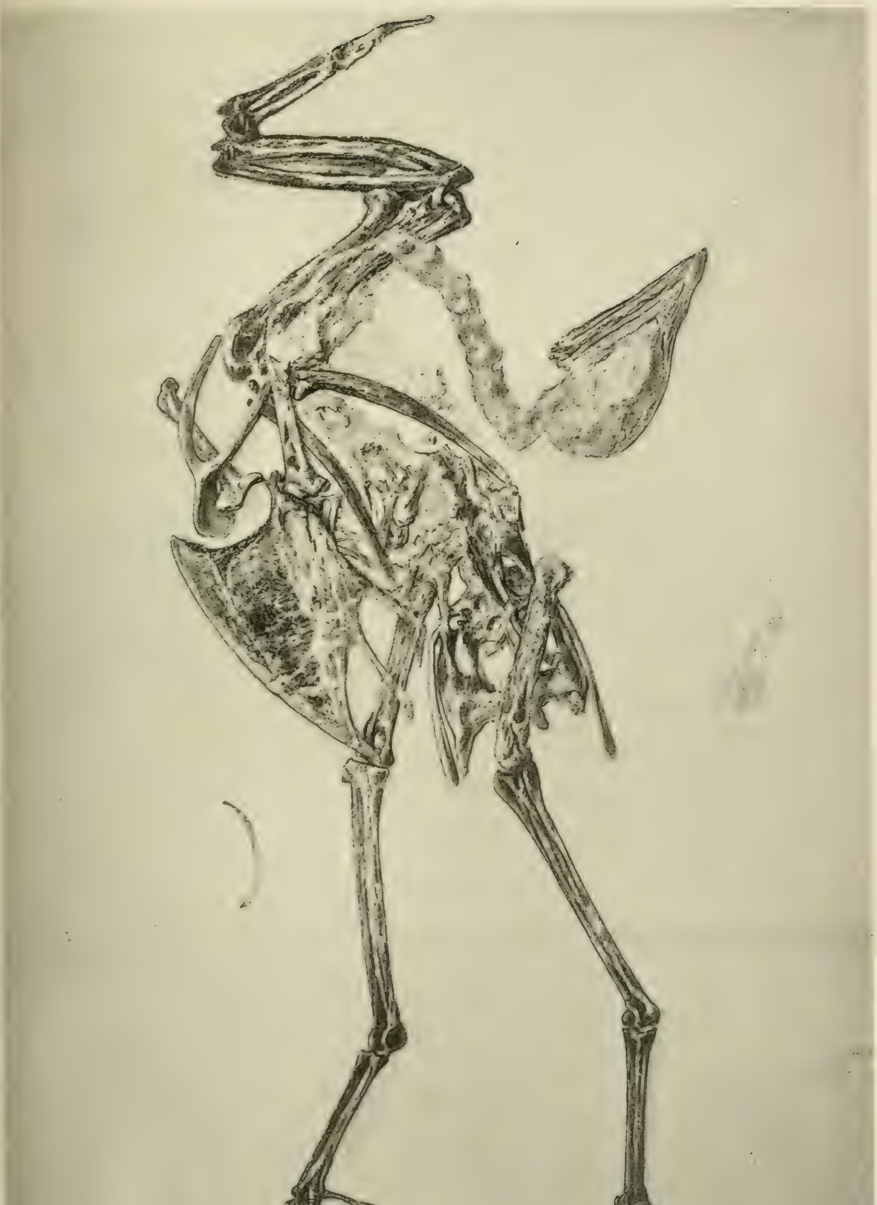
Cracine Characters. — Blunt, upright, subtriangular costal process, shallow inner sternal notch, small prepubis, proportions of pelvis, elongate tarsus with all the toes on the same level.

Peculiar Characters. — Absence of recurved mandibular process; short, stout, U-shaped furcula with large hypocleidium and articular facet for coracoid.

The weight of the peculiar characters, particularly the absence of a post-angular process, are, as stated in the introductory remarks, sufficient to prevent the bird being placed in either the Cracidæ or Megapodidæ, thus necessitating the establishment of a new family, Gallinuloididæ. The principal family characters are the absence of a postangular mandibular process, presence of an articular facet on the furcula for the reception of the acrocoracoid, and the presence of an acrocoracoid.

The generic characters are considered to be the stout U-shaped furcula, the shape of the scapula, and the anterior extent of the *crista sterni*. As specific characters are always comparative, none can be formulated from a single specimen, even did they not depend to so great an extent in birds — often entirely — on external features.

This bird is interesting not because it presents any striking peculiarities of structure, but rather because it does not, and because it belongs, as we might naturally expect from its age, to a generalized type having points of structural resemblance with various families of gallinaceous birds. It is an additional reminder, were any needed, of the great gaps in our knowledge of the development of birds and of the rapidity with which they attained their present forms. The mammals of the Eocene are quite different from existing species, but this bird readily takes its place among the forms of to-day.



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THE DEVELOPMENT OF THE MOUTH-PARTS OF ANURIDA MARITIMA GUÉR.

BY JUSTUS WATSON FOLSOM.

WITH EIGHT PLATES.

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No. 5.— *The Development of the Mouth-Parts of Anurida maritima Guer.*[1] By Justus Watson Folsom.

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Introduction.

Our present ideas of homology in the details of insect mouth-parts rest almost exclusively upon anatomical data, and need careful revision in the light of embryological facts.

Too many entomologists have speculated upon the subject in complete disregard of evidence from ontogeny or phylogeny. Embryologists, on the other hand, have greatly neglected the mouth-parts.

It seems almost superfluous to insist that highly specialized organs can be but imperfectly understood unless studied in egg and larva as well as imago; that generalized types illuminate specialized forms; and that equivalent groups are linked together through their more generalized members; yet too often these accepted principles are not applied.

The objects of the present paper are two: first, to supplement my previous account (Folsom, '99) of the anatomy and functions of the mouth-parts of a representative Collembolan; second, to discuss the morphology of mandibulate mouth-parts of insects and their nearest allies upon anatomical and embryological evidence derived from the most primitive insects, the Apterygota.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. 114.

My comparisons have been hindered by the scanty and fragmentary nature of published embryological observations upon the mouth-parts of Arthropods. Detailed studies upon the subject in the less specialized Pterygota, Crustacea, Arachnida, Diplopoda, and Chilopoda do not exist, but are necessary for the proper understanding of the morphology of the mouth-parts, and will have much bearing upon the phylogeny of the classes named.

The present study was made under the supervision of Dr. C. B. Davenport, to whom I am most grateful for his constant, critical supervision, valuable advice and encouragement.

Professor E. L. Mark has carefully revised the text and attended to all the details of publication; his help, as always, has been of inestimable value to me.

Methods.

For killing eggs, and adults as well, simply hot water was used, with excellent results. After killing, material was carried through several successively stronger grades of alcohol and finally preserved in absolute alcohol.

In the study of the embryo, both dissections and serial sections were made. As much as possible was learned by dissection, as that method, although difficult, gave more trustworthy results than could possibly be obtained by reconstruction from sections. The germ bands of freshly killed embryos were too delicate to be dissected out uninjured; but after being in absolute alcohol for two months they had become sufficiently hardened for this operation. A longer stay made them brittle, but advantageously so in some respects.

Dissections were made under a compound microscope with a magnification of about one hundred and fifty diameters. For the finest work, the "minutien Nadeln," used by entomologists for pinning minute insects, were employed. The general form and position of an embryo could be seen through the transparent egg-membranes; but to get clearer views, the outer membrane was removed, the remaining corrugated membrane punctured, and a staining fluid allowed to penetrate the germ band. Preparatory to the dissection of minute structures, the egg was placed in weak glycerine, which caused the embryo to shrink away from the membranes slightly, allowing these to be removed; the germ band was dissected out and stained with Grenacher's alcoholic borax-carmine or hæmatoxylin. Isolated parts of the embryo were mounted temporarily in weak glycerine without pressure, in such a way that by moving the cover glass they could be rolled into various desirable positions.

For sectioning, portions of the embryo, or punctured eggs, were imbedded in hard paraffine. The eggs required at least four hours for thorough penetration. For orienting, Woodworth's ('93) method was employed, but not always with success, as the objects were liable to become distorted or even lost. A simpler, but more efficient, method for these particular objects was to orient them under the compound microscope with a hot needle in a glycerine-smeared watch-glass of melted paraffine, and to fix them in place by touching the glass beneath with cold water before hardening the paraffine throughout. When the block of paraffine was inverted under the compound microscope, the imbedded object could be seen through a thin film of paraffine, and a scratch could be made to indicate the plane of sectioning.

Sections from 5 to 10 μ in thickness were cut with either a Reichert or a Minot-Zimmermann microtome, fastened with Mayer's albumen mixture, and stained with various reagents, chiefly Delafield's or Kleinenberg's hæmatoxylin followed by safranin, Grenacher's alcoholic borax-carmine, and Heidenhain's iron-hæmatoxylin.

General Description of Egg.

The eggs of Anurida maritima are spherical, from 0.26 mm. to 0.38 mm. in diameter, enlarging with age, and at first light yellow, later becoming orange.

They occur abundantly along the Atlantic coast under stones between tide-marks, and are usually mingled with the conspicuous white exuviæ of the parents.

The eggs of Collembola depart widely from those of other insects by being holoblastic; they are slightly unequal in cleavage. After the morula stage the outer nuclei and accompanying protoplasm migrate toward the periphery, leaving behind yolk masses and also cells which subsequently prove to be entodermal. The peripheral cells become arranged in two layers: the ectoderm, a continuous superficial layer, with nuclei at regular intervals, and the mesoderm, an inner, less compact layer with fewer and scattered nuclei. Thus there soon results a condition like that derived from superficial cleavage. The ventral plate, or germ band, is formed by migrant mesoderm cells, and, according to Uzel ('98, p. 22, Tomocerus), is first represented by two pairs of isolated thickenings, — the procephalic and mandibular fundaments. I have found that the appendages appear in succession from in front backward, and that they are well developed long before the segmentation of the germ band. The blastoderm is interrupted only by the "dorsal organ," which is attached to the inner egg membrane.

Claypole ('98, pp. 255–258) distinguishes five egg membranes in Anurida, and maintains that all arise from the egg or the blastoderm. I find that in the ripe egg two are evident: a thick outer and a thin corrugated inner one, respectively analogous to, if not homologous with, the chorion and the vitelline membrane of other insects. Another delicate membrane completely envelops the embryo in early stages (Plate 1, Figures 1, 3, *mb.*), except where interrupted by the dorsal organ. I have found it to be, not a "larval skin," but a blastodermic membrane.

The peculiar cleavage of Collembola has been observed by Oulganine ('75, '76), Lemoine ('83), Claypole ('98), and Uzel ('98). In the most nearly related group, Thysanura, the cleavage has been shown to be superficial by Grassi ('85), Heymons ('96, '97^a), and Uzel ('97, '98). In cleavage, then, Collembola resemble many Crustacea and Arachnida, in which it is at first total and secondarily superficial.

Thysanura, on the other hand, approach the Orthoptera, in that the cleavage is from the first superficial.

The "dorsal" or "precephalic" organ of Collembola has been described by Lemoine ('82), Wheeler ('93), Claypole ('98), and Uzel ('97, '98); of Thysanura, by Grassi ('85), Heymons ('96, '97^a), and Uzel ('97, '98). Wheeler homologized it with the "indusium" of Orthoptera, and suggested its analogy with the embryonic sucking-disk of Clepsine. Claypole collected evidence of a similar structure in Crustacea, which has been reinforced by Uzel.

Reference Stages.

For descriptive purposes I have selected nine consecutive stages of development, which may be identified in the entire egg by the following characteristics: —

At Stage 1 (Plate 1, Figure 1) the embryo is almost spherical with all the primary appendages represented by small papillæ. The dorsal organ is large, with a spherical imbedded portion and an expanded superficial part, the latter firmly attached to the corrugated membrane. This stage is very nearly that of Claypole's ('98, Plate XXIII.) Figures 40 and 41 of the same species.

Stage 2 (Plate 1, Figure 2) is characterized by folds representing the last five abdominal segments, and by longer appendages, of which the antennæ and legs show traces of segmentation. It is approximately the stage of Figures 42 and 47 of Claypole.

At Stage 3 (Plate 1, Figure 3) the ventral surface of the embryo is almost flat, preparatory to involution; the legs are decidedly longer, and the fundament of the proctodæum is distinct. Figures 43 and 43^a of Claypole belong near this stage; also Figure 10 of Ryder ('86), likewise for Anurida maritima.

During Stage 4 (Plate 1, Figure 4) the germ band is folding into the yolk, the fold beginning anteriorly and continuing backward. The antennæ and legs are long and stout. My figure shows a stage a little later than that of Figure 44 by Claypole.

At Stage 5 (Plate 1; Figure 5) the involution has reached the centre of the egg, the antennæ and legs are distinctly segmented, the mouth-folds are conspicuous, and the dorsal organ has shrunken considerably.

Stage 6 (Plate 1, Figure 6) is much like the last, except that the head and tail of the embryo have approached each other. The dorsal organ is much reduced and somewhat flask-shaped. This is the stage of Ryder's Figure 7.

At Stage 7 (Plate 2, Figure 7) the eyes are first recognizable as five black circular patches on either side. Figure 45 of Claypole represents this condition.

Stage 8, which I have not figured, differs externally from the last in that the number of eyes is no longer evident, it being obscured by a suffusion of pigment. The degenerating dorsal organ now disappears by resorption.

Stage 9 (Plate 6, Figure 41; also Claypole, Figure 48) refers to the newly hatched insect. Before this period, movements of the insect may be seen through the egg membranes. If eggs have been kept dark, — the normal condition, — the emerging insects are white, excepting the eyes; if exposed to sunlight, however, the embryos become blackish-blue long before hatching. At emergence the external clothing of setæ is complete, and the mouth-parts are fully formed.

Procephalic Lobes.

The fundaments of the procephalic lobes are two isolated thickenings of the blastoderm, which are the first of the paired fundaments to appear. Each procephalic fundament is lenticular in form and rapidly increases in thickness and area. In the earlier stages the procephalic thickenings are not definitely circumscribed, but merge insensibly with the rest of the blastoderm.

Previous to Stage 1 the procephalic lobes meet in the median plane, where the labral fundament then appears. Before the appearance of the labrum, however, the antennal fundaments evaginate from the posterior regions of the procephalic lobes.

In Stages 1 and 2 (Plate **1**, Figures 1 and 2) the lobes continue to increase in area and thickness.

At Stage 3 either lobe is relatively as thick as is represented in Figure 3, *pr'ceb.*, and in lateral surface views (Plate **2**, Figures 9, 10, *pr'ceb.*) appears as a strongly convex, oval protuberance.

In Stages 4 (Plate **3**, Figure 12, *pr'ceb.*) and 5 (Plate **3**, Figures 19, 20, 21, *pr'ceb.*) the procephalic lobes change little except in size, and the median depression between them (*sul.*) is still distinct.

In Stage 7 (Plate **5**, Figure 30) the depression (*sul.*) becomes obliterated, and the eyes (Plate **4**, Figure 24, *ocl.*) and postantennal organs (Figure 24, *o.p'at.*) appear. At this stage sections show a pair of ganglionic fundaments (Plate **4**, Figure 28, *pr'ceb.*), the largest and most anterior in the head, with which the next two pairs eventually unite to form the supra-œsophageal ganglion of the adult (Plate **8**, Figure 51, *gn.su'œ.*).

In other Collembola the procephalic lobes develop in just the same way, as may be gathered from Nicolet (**'42**, Smynthurus), Packard (**'71**, Isotoma), Lemoine (**'83**, Smynthurus), and Uzel (**'98**, Tomocerus).

Also in Campodea the same course of development is followed (Uzel, **'98**, Taf. 3, Figures 33–36; Taf. 4, Figures 37–42) as well as in Lepisma (Heymons, **'97**^{a}).

In fact, the simple process described for Anurida characterizes not only Orthoptera (Ayers, **'84**, Wheeler, **'93**, Heymons, **'95**), but also insects in general.

The procephalic lobes of Diplopods and Chilopods develop essentially as in insects and Crustacea, but no detailed comparisons can be made as yet.

The most interesting considerations concerning the ocular segment of Hexapoda relate to its equivalence with the first segment of Crustacea.

Viallanes (**'87**, pp. 98–109) has carefully compared the brain in both classes and found a striking agreement, extending to histological details:

"Considérons en premier lieu la partie latérale du protocérébron, connue des anatomistes sous le nom de ganglion optique; elle nous montre d'abord, en allant de dehors en dedans, les parties suivantes: les fibres post-rétinennes, la lame ganglionnaire, le chiasma externe, la masse médullaire externe, le chiasma interne et la masse médullaire interne.

"Toutes ces parties, si nettement caractérisées, se retrouvent sans modification chez l'Insecte ; il n'est donc pas douteux qu'il existe au moins pour cette première région du ganglion optique similitude complète entre les deux types que nous cherchons à comparer. . . . Cette similitude a été reconnue par tous ceux qui se sont occupés de ce sujet (Berger, Bellonci, Carrière et moi). . . . En somme, au point de vue des parties dont nous venons de parler, il n'existe que des différences bien peu importantes entre l'Insecte et le Crustacé : chez le premier, les deux lobes cérébraux sont très rapprochés et se soudent sur la ligne médiane ; chez le second, ces mêmes parties (appelées balles supérieures) sont écartées, chacune d'elles étant logée dans le pédoncule oculifère correspondant."

Packard '**98**, p. 51) says, "Hence the ocular segment, *i. e.*, that bearing the compound and simple eyes, is supposed to represent the first segment of the head. This, however, does not involve the conclusion that the eyes are the homologues of the limbs, however it may be in the Crustacea." As Viallanes has proved the equivalence of protocerebrum and optic nerves in insects with those of Crustacea, and others have shown that the compound eyes of both groups are constructed alike, even to the number of retinal elements, it is proper to infer that the compound eyes of the two groups are homologous.

The protocerebrum of Collembola and Thysanura agrees in development and structure with that of other insects and also with decapod Crustacea ; the facetted eyes of Hexapoda and Crustacea are likewise homologous.

Labrum and Clypeus.

The labrum is chiefly interesting because it has frequently been held to represent a pair of primary appendages.

At Stage 1 (Plate **1**, Figure 1 ; Plate **2**, Figures 8, 8^a, *lbr.*) the labrum (really clypeo-labrum) is a median hemispherical papilla anterior to and distant from the bases of the antennæ ; at no period does it give evidence of a paired origin.

At Stage 2 (Figure 2), while the distances between the labrum and mandibles is precisely the same as in the preceding stages, the antennæ are inserted beside the oral region of the upper lip ; the latter is globular and flattened against the egg shell.

Surface views at Stage 3 (Figure 3) are given in Figures 9, 10, and 11, *lbr.*

A sagittal section at this stage shows (Plate **3**, Figure 13) an elongation of the labral fundament, and demonstrates its origin from the germ band by simple evagination. The posterior surface of the labrum is now the anterior wall of a distinct invagination (*or.*), the fundament of the stomodæum.

At Stage 4 (Figure 4) the labrum is longer (Plate **3**, Figure 19, *lbr.*) and its long axis has swung backward, probably on account of the excessive elongation of the anterior labral surface. A ventral aspect of the germ band (Figure 12) shows the labrum to be approximately oval in cross-section, but with a more rounded anterior surface.

At Stage 5 (Figure 5) the labrum (Plate **3**, Figure 20, *lbr.*) is decidedly longer. The basal part of the labral fundament represents the clypeus, with which the lateral folds, or mouth-folds (Figure 21, *pli.or.*) are now confluent; overhung by the end of the labrum is the distinct stomodæum.

At Stage 7 (Figure 7) a distinct depression (Plate **5**, Figure 31, *dep.*) separates the clypeus from the procephalic lobes; the depression, in fact, may be seen as early as Stage 1, for it simply forms the angle between the labral fundament and the procephalic lobes. Although the clypeus merges insensibly into the cheeks, the labrum is a free trapezoidal plate, as in the adult (Plate **6**, Figure 40, *lbr.*). The antennæ are now inserted (Plate **4**, Figure 24, Plate **5**, Figure 30, *at.*) almost exactly opposite the base of the labrum. At this stage the clypeo-labral suture is not distinctly indicated (Figure 24), but in Stage 8 an invagination occurs to form the labral hinge of the adult (Plate **6**, Figure 40, *atc.*).

In Stage 8 the only other important changes in the labrum are the evagination of single hypodermis cells to form the external setæ, and the formation of trivial cuticular folds which represent the rudiments of the epipharynx. In Anurida, as in Orchesella, the epipharynx is purely a cuticular structure and unconnected with the central nervous system.

In the adult Anurida a shallow clypeo-frontal groove is distinguishable (Plate **6**, Figure 40, *sul.*), but does not amount to a suture, and the clypeus is not laterally demarcated from the groove. In Orchesella and Tomocerus, however, the clypeus is a distinct sclerite. In none of the Collembola that I have studied is there any distinction between clypeus and labrum on the roof of the pharynx.

Packard (**'71**, p. 18) says, regarding Isotoma, "The clypeus, however, is merged with the epicranium, and the usual suture between them does not appear distinctly in after life, though its place is seen in Figure 13 to be indicated by a slight indentation. The labrum is distinctly defined by a well-marked suture, and forms a squarish knot-like protuberance, and in size is quite large compared to the clypeus. From this time begins the process of degradation, when the insect assumes its Thysanurous characters, which consist in an approach to the form of the Myriapodous head, the front, or clypeal regiòn being reduced to a minimum, and the antennæ and eyes brought in closer proximity to the mouth than in other insects."

Lemoine (**'83**, p. 510, Planche XV., Figure 24) mentions in Smynthurus, "Les deux appendices qui constitueront la lèvre supérieure," but they appear in his figure as only simple lobes from a large, median labrum.

Wheeler (**'93**, p. 57, Figure VI.) represents the labrum of Anurida as a median, unpaired fundament, and Claypole (**'98**, Plate XXIII.) gives several surface views of the upper lip in the same species.

Uzel (**'98**, Taf. VI., Figur 87) shows the single labral fundament of Macrotoma (Tomocerus).

Regarding Campodea, Uzel (**'98**, p. 26) says: "Vor der Mundeinsenkung erblickt man jetzt schon die unpaare Anlage der Oberlippe," and partially illustrates (Taf. IV., VI.) the development, which proceeds essentially as in Anurida.

The finished labra of Campodea (Grassi, **'86^b**, Tav. IV., Figura 7) and Japyx (Grassi, **'86^b**, Tav. II., Figura 15 *bis*) are very simple rounded plates.

For Lepisma, Heymons (**'97^a**, Taf. XXX.) figures the labral fundament as a prolongation from the procephalic lobes, and characterizes it (p. 591) as "eine kleine, vollkommen, ungetheilte, einfache Platte." Later (p. 593) he says, "Die Oberlippe wird bedeutend grösser und bekommt an ihrem hinteren Rande eine mediane Einkerbung (Figure 17)." The median indentation is clearly, however, a secondary formation.

In both Lepisma and Machilis (Oudemans, **'88**, Taf. I., Figur 3) the labrum remains simply an anteriorly rounded plate.

In the Orthopteran Œcanthus, Ayers (**'84**, p. 240, Plate 18, Figures 21, 22) describes the unpaired fundament which forms the ovate labrum. In short, the labrum in all Orthopteran families develops from an unpaired fundament. (See Wheeler, **'93**, Heymons, **'95^b**.)

The same is true of the Libellulidæ and Ephemeridæ (Heymons, **'96**, Taf. II., Figuren 19, 29), and examples might be multiplied to show that the labrum does not represent a pair of appendages. The view held by Kowalevsky, Carrière and others, that it did, was based chiefly upon anatomical evidence, which has since been disproved by Heymons ('95) and others. (See Packard, '98, pp. 42–43.)

Scolopendrella (Latzel, '84, p. 8, Taf. I., Figur 4; Grassi, '86^a, p. 15, Tav. II., Figura 6) has a simple, emarginate, six-toothed labrum, and, like Hexapoda, a distinct, subtriangular clypeus. Moreover, as Packard ('98, p. 22) has affirmed, it has a V-shaped tergal suture, which exists also in the more generalized insects, but is absent in Myriopods.

In Diplopoda, an upper lip is present as a transverse plate, fused, however, with the cranium.

In Chilopoda, a similar labrum is present, but is not always basally fused, and frequently consists of three transversely placed sclerites. It originates as a simple median lobe (Heymons, '97^b, p. 4, Figur 1, Scolopendra).

In Crustacea the upper lip is derived from a median, unpaired evagination corresponding almost exactly in position with the labral fundament among insects.

Among insects, then, the labrum and clypeus develop from a median evagination between the procephalic lobes, and give no satisfactory evidence of paired origin. The same statement applies also to Crustacea, and, as far as is known, to Myriopods.

Antennæ.

The antennæ are the first paired organs to appear. They develop from the posterior boundaries of the procephalic lobes, and at Stage 1 (Plate 1, Figure 1, Plate 2, Figure 8, *at.*) are stout cylindrical papillæ already faintly constricted into two segments. As Figure 8 shows, they are more lateral than the other paired fundaments, and at first far behind the labrum. Sections prove them to be simple ectodermal evaginations, like all the other appendicular fundaments.

At Stages 2 and 3 (Plate 1, Figures 2, 3, *at.*) the antennæ are longer and usually composed of three segments. In Figure 2 the fourth segment, which normally appears later than Stage 2, is suggested. They have now moved forward to positions near the labrum; in Stage 4 (Plate 1, Figure 4; Plate 3, Figure 12, *at.*) they lie on the two sides of that appendage, and in Stage 5 (Plate 1, Figure 5; Plate 3, Figure 21, *at.*) they have attained a position farther forward than the upper lip.

In Stage 6 (Plate **1**, Figure 6, *at.*) there is clearly indicated a fourth antennal segment, which in Stage 7 (Plate **2**, Figure 7; Plate **4**, Figure 24, *at.*) becomes more distinct. At this time the antennæ are long and stout, and occupy a position still farther forward than before.

At hatching (Plate **6**, Figure 41) they are pre-oral, more slender, distinctly segmented, and clothed with setæ.

Elongation of the antennæ occurs throughout their entire length, judging from the number of cells in longitudinal alignment on the same segment at different stages of growth, and also from the frequency of karyokinesis in different parts of the appendage. Growth is more rapid, however, in the apical region, from which the segments are successively constricted. In all the oral fundaments, in fact, growth was inferred to be most rapid at the apex, although likewise occurring throughout the rest of the ectodermal layer. At the apex itself — and these remarks apply equally well to the legs — the hypodermal cells are larger and more turgid than elsewhere, projecting as minute lobes from the surface. The chromosomes are very small, but frequently so arranged as strongly to suggest mitotic division.

At Stage 5 (Plate **4**, Figure 28, *deu'ceb.*) an antennary ganglion supplying the antennal nerves, becomes evident, but finally fuses with the first and third ganglia, between which it lies, to form the supraœsophageal ganglionic mass.

In Thysanura the antennæ develop essentially as I have described for Collembola, being likewise at first post-oral and subsequently pre-oral, as Uzel ('**98**) has shown for Campodea and Heymons ('**97**^{a}) for Lepisma. Such a migration of the antennæ is, however, not peculiar to Apterygota, but is characteristic of all insects.

Among Diplopoda but a single pair of antennal fundaments occurs (Heymons, '**97**^{b}, p. 7, Figur 2, Glomeris). Judging from their position in relation to the mouth, they are equivalent to the antennæ of Chilopoda, among which Heymons ('**97**^{b}, p. 4, Figur 1, Scolopendra) has discovered two pairs of antennal fundaments. The præ-antennal rudiments in Chilopoda appear to represent the antennæ of insects and the antennules of Crustacea, the second pair to be equivalent to the intercalary appendages of insects and the antennæ of Diplopods and of Crustacea.

It can scarcely be doubted, in view of the researches of Viallanes ('**87**), that the antennæ of insects are homologous with the antennules of Crustacea. In the author's words ('**87**, p. 105): "Voyons maintenant le deuxième renflement cérébral du Crustacé décapode. Il est formé d'une

paire de masses nerveuses ventrales connues sous le nom de *lobes olfactifs*, réunies l'une à l'autre par une commissure transverse, et d'une paire de masses dorsales qu'on pourrait désigner sous le nom de lobes dorsaux.

"Les lobes olfactifs ont une structure tout à fait spéciale; la substance ponctuée qui entre dans leur constitution est, pour ainsi dire, 'segmentée' en un grand nombre de petites boules d'aspect absolument caractéristique, qu'on désigne sous le nom de *glomérules olfactifs.* Les lobes dorsaux, au contraire, n'ont dans leur structure rien qui soit spécifique.

"Le nerf antennaire naît du deuxième renflement cérébral par deux racines, — l'une sort du lobe olfactif, l'autre du lobe dorsal; ce dernier, en outre, donne naissance à un nerf tégumentaire.

"Cette description du deuxième segment cérébral du Crustacé peut, et sans qu'il y ait aucun changement à y faire, s'appliquer à l'Insecte, tant il y a au point de vue de cette région cérébrale similitude entre les deux types. Nous sommes donc en droit d'exprimer cette similitude, en appelant du même nom de *deutocérébron* le deuxième segment cérébral, qu'il s'agisse d'un Crustacé on d'un Insecte."

In favor of contrary views little can be said. "Arguments drawn from the absence or presence of either pair of antennæ in the higher Crustacea are not convincing, as there is great variation in the degree of development of their appendages in different groups" (Claypole, '98, pp. 265–266). Thus, in some Amphipods, the antennules are short, and in certain Isopods, extremely reduced. On the other hand, as Claypole notes, it is suggestive that in the generalized genus Apus, the first antennæ are constant and the second variable or absent.

The fact that the antennules of decapod Crustacea cannot be called "post-oral" in origin, is not as significant as it may appear to be. The antennules originate at the side of the labrum (Reichenbach, '86), nearly post-orally, and migrate forward. In view of all other fundamental correspondences between hexapod antennæ and crustacean antennules, the trifling difference in original position may be ignored, especially as the organs in question are eminently migratory.

I believe, therefore, that the deutocerebrum of Apterygota, representing the second somite, is homologous with that of Orthoptera and other insects.

Premandibular Appendages.

The little-known "premandibular" or "intercalary" appendages are important as bearing upon the larger and much-disputed question of the segmentation of the head.

In Anurida, they are visible in Stages 1 and 2 only, as slight thickenings of the germ band, which are often ill defined in outline and hardly deserve the name of appendages. In fact, their demonstration is largely a matter of technique. I dissected over thirty germ bands for this purpose, stained them variously, and mounted them temporarily in weak glycerine, without finding more than suggestions of the intercalary appendages. At this point, Miss Claypole most kindly sent me some preparations which were a little clearer than any I had made. These I imitated by staining with Delafield's hæmatoxylin, decolorizing with acid alcohol and mounting without pressure in xylol balsam. If care is taken in decolorizing, a condition may be obtained in which all of the germ band between the antennæ and mandibles has lost color excepting a rather vague patch on either side, usually not as distinct as in Plate **2**, Figure 8^a, *app. pr'md.* These patches are so slightly, if at all, elevated that they are not distinguishable with certainty in transverse or sagittal sections of the germ band. In good preparations, the lateral boundary of either appendage is indicated by a curving row of ectodermal nuclei, and this resemblance to the other paired fundaments is further shown in the presence of an imperfectly developed core of mesodermal nuclei (Figure 8^a, *ms'drm.*).

Wheeler and Claypole have represented the appendages much smaller than I have, and appear to have figured the mesodermal core only. In none of Miss Claypole's slides are the appendages outlined as sharply as in the preparation from which my Figure 8^a was made. In glycerine the yolk granules interfere with proper observation, but in balsam this disadvantage is removed.

Although the appendages are extremely rudimentary, the evidence they furnish of the presence of an intercalary segment is reinforced by the condition of the nervous system, for there is at Stage 5 a small neuromere (Plate **4**, Figure 28, *tri'ceb.*), which, from its relation to the remaining cephalic neuromeres, must be regarded as belonging to the premandibular segment. It ultimately fuses with the deutocerebrum to form a part of the supraœsophageal ganglion.

Viallanes first called attention to the tritocerebral segment of insects and Crustacea; he was afterwards supported by Wheeler, who found that it bore a pair of appendages in Anurida; thus Wheeler ('**93**, p. 57, Figure VI.) discovered the intercalary appendages in this species, and indicated their obscurity by representing them by broken circles. Claypole ('**98**, p. 263, Plate XXIII., Figures 40, 47) also observed the appendages, but erroneously inferred that they became modified to form the sides of the face, — a view which I shall discuss presently.

A somewhat similar pair of appendages in the embryo of Apis was long ago observed by Bütschli (**'70**), and a few years later by Grassi (**'85**) also; but Packard (**'98**, p. 52, Figure 35) questions whether these belong to the category of segmental appendages.

Heymons (**'95**^{b}, Taf. I., Figur 5) also has recognized the "Vorkiefersegment" in Orthoptera. He says (**'95**^{a}, p. 16): "Letzteres [Vorkiefersegment] kommt, wie schon gesagt, überhaupt nur in ganz rudimentärer Weise zur Anlage. Extremitäten treten an ihm nicht mehr auf. Sein Ganglion rückt nach vorn und geht in die Formation des Gehirns ein. Bei dieser Gelegenheit werden zugleich auch die äusserlich wahrnehmbaren Spuren des Vorkiefersegments verwischt. Selbst im Innen liegen die Verhältnisse nicht viel günstiger. Das Mesoderm des Vorkiefersegments bildet nämlich bei den Orthopteren ein eigenartiges Organ, den sogennantes Suboesophagealkörper, welches ebenfalls nur eine provisorische Bedeutung besitzt und später zu Grunde geht."

The same author (**'97**^{a}, p. 590, Figur II.; Taf. XXX., Figuren 17, 20), referring to the embryo of Lepisma, writes (p. 591), "Genau auf der Grenze zwischen dem verbreiterten vorderen Kopfabschnitt und dem darauf folgenden verjüngten Körpertheil zeigen sich ferner zwei, allerdings nur schwach markirte, laterale Verdickungen (*Trc.*). Dieselben kennzeichnen die Region des rudimentären Vorkiefer- (Intercalar) Segmentes. An diesen Segmente kommen während der Entwicklung von Lepisma Extremitäten nicht zur Ausbildung." This nearly agrees with the condition in Anurida.

Uzel records distinct intercalary appendages for Campodea in his preliminary paper (**'97**^{b}, p. 232), and in his final work (**'98**, p. 26) says: "Sehen wir auf dem sogenannten Intercalarsegmente (Vorkiefersegmente), das sehr deutlich entwickelt ist, jederseits eine kleine Erhöhung auftreten (*int.*), welche als die Extremitätenanlagen dieses Segmentes zu deuten sind." (p. 37.) "Die Extremitäten dieses Segmentes werden bei Campodea in Form zweier Höcker angelegt, welche sich, wie wir voraussenden wollen, bis in das geschlechtereife Alter erhalten, und hier als Bestandtheile der ausgebildeten Mundwerkzeuge fungieren (der einzige bekannte Fall unter dem Insecten), indem aus ihnen kleine, praeoral gelegene, beiderseits an der Wurzel der Oberlippe befindliche Lappen (die Intercalarlappen, Taf. VI., Fig. 85, *int.*) entstehen. Bei Lepisma sind keine Extremitätenanlagen auf dem Intercalarsegmente vorhanden." . . . "Unter den Myriopoden wurden von Zograf bei den Embryonen von Geophilus ziemlich weit hinter dem Munde und dicht vor den Anlagen der Mandibeln zwei ansehnliche Höcker beschrieben und abgebildet, welche wahrscheinlich den Höckern auf dem Intercalarsegmente von Campodea homolog sind. Sie werden nach dem erwähnten Autor immer kleiner und kleiner und sollen endlich ganz verschwinden."

In Anurida the intercalary thickenings become involved in the folds which form the sides of the face, as I shall describe, but I believe they are not, as Miss Claypole held, the fundaments of those folds.

In Tomocerus and Orchesella (Folsom, '**99**, p. 14, Plate **2**, Figure 9) I have found that "at either end of the [labral] hinge . . . the cuticula is swollen into a conspicuous chitinous lobe, which projects into the pharynx to fit against a corresponding prominence of the mandible," etc. As these lobes in the adult occupy precisely the same positions as those of Campodea (Uzel, '**98**, Taf. VI., Figur 85, *int.*), I believe them to be intercalary appendages. In Anurida no such lobes exist.

In Chilopods, two pairs of antennal fundaments appear (Heymons, '**97**^{b}, p. 4, Figur 1, Scolopendra), and the second, which alone become functional, are equivalent in position to the intercalary appendages of Apterygota as well as the antennæ of Diplopods (cf. Heymons, **97**^{b}, p. 7, Figur 2, Glomeris).

The equivalence of the tritocerebrum in Hexapoda and Crustacea was first shown in detail by Viallanes. His account ('**87**, pp. 105–108) is too long to be quoted in full, but he concludes: "Les deux lobes constitutifs du tritocérébron de l'Insecte, et que j'ai désignés sous le nom de lobes tritocérébraux, représentent exactement les deux ganglions œsophagiens du Crustacé; ils donnent naissance aux mêmes racines nerveuses, ils sont, comme ces derniers, unis *au-dessous* de l'œsophage par la commissure transverse de l'anneau œsophagien."

Many authors (Korschelt und Heider, '**90–93**, p. 906) agree in homologizing the antennæ of Hexapoda, innervated from the deutocerebrum, with the first antennæ of Crustacea; also in homologizing the mandibles of both groups. Therefore only the intervening appendages of the tritocerebrum remain to represent the second antennæ of Crustacea.

An intercalary segment, then, is to be recognized among Pterygota, at least in the more generalized forms, and especially among the primitive Apterygota, and in the latter group it may bear rudimentary appendages, even in the adult. The intercalary segment is to be regarded as equivalent in morphological value to any primary head-segment, — especially because it bears a primitive ganglion, — and it constitutes the third head somite. The tritocerebrum of Hexapoda is equivalent to that of decapod Crustacea, and the intercalary appendages of the former are homologous with the second antennæ of the latter, and probably with the antennæ of Chilopoda and Diplopoda.

Mandibles.

The fundaments of the mandibles appear in Stage 1 (Plate **1**, Figure 1, *md.*; Plate **2**, Figure 8) as a pair of sub-hemispherical papillæ behind the antennæ, and considerably nearer than they to the median plane. At Stage 2 (Plate **1**, Figure 2, *md.*) they are longer and bluntly conical; but at Stage 3 (Plate **1**, Figure 3; Plate **2**, Figure 9, *md.*) in lateral aspect they appear shorter than before, because the base is covered by a lateral fold of the germ band (Figure 9, *pli. or.*). Sections through the mandibles transverse to the germ band (Plate **3**, Figure 16) show that they are low broad ectodermal evaginations containing mesoderm. In Stage 4 (Plate **1**, Figure 4; Plate **3**, Figure 19, *md.*) the mandibles, although they have become long and cylindrical, are largely covered by the lateral folds (*pli. or.*) which have grown more rapidly than they; and in the following stage (Plate **1**, Figure 5; Plate **3**, Figure 20, *md.*), though still nearly perpendicular to the germ band, they are almost completely covered laterally by the folds. The mutual relations of mandibles and folds are shown in transections of the germ band (Plate **4**, Figure 23), in which it may also be seen that the mandibles (*md.*) are swollen at their ends, their lateral surfaces conforming to the adjacent surfaces of the folds (*pli. or.*). The long axes of the mandibles converge at their bases toward the median plane, and it is noteworthy that the lateral surface of each mandible is distinctly longer than the mesal surface (Figure 23, *md.*) — a foreshadowing of the oblique orifice of the finished organ.

At Stage 7 (Plate **2**, Figure 7; Plate **4**, Figure 24, *md.*) the mandibles, now wholly covered by the lateral folds (*pli. or.*), are much longer and still conical; they are shorter and much more slender than the underlying first maxillæ; and instead of being perpendicular to the germ band, they have now swung forward through an angle of almost ninety degrees; moreover, they converge in front toward the median plane, as do the first maxillæ (Plate **5**, Figure 29). In this stage the mandibular muscles are individually distinguishable (Figure 32), and the anterior extremity of the mandible bears several minute lobes (Figure 32), each consisting of a single hypodermal cell. In the next (8th) stage the free end continues to bend toward the median plane until the apices of both mandibles meet. The terminal unicellular lobes become multicellular and secrete the incisive teeth (Plate **6**, Figure 37 *de. i'cis.*), of which there are finally five principal ones on the right and six on the left mandible. Although the "head" of the completed organ is almost solid chitin (Plate **6**, Figure 37), there are five canals, one penetrating the base of each tooth; the hypodermal cells have, however, receded from the "head."

The extreme basal end of the finished mandible is prolonged as a chitinous, conical projection (Plate **6**, Figure 36, *cdx.*), which, as in Orchesella, is let into a concave chitinous piece that I have called the stirrup (*sta.*), from which it may be withdrawn when the mandibles are protruded. This projection, or pivot, arises in Stage 7 (Plate **5**, Figure 32, *cdx.*) as a hypodermal evagination of the mandibular fundament, and simultaneously the chitinous stirrup (*sta.*) is formed in a transverse, superficial groove of the hypodermis lining the pharyngeal pocket in which the mandible lies. In Orchesella the lateral end of the stirrup unites with the external cuticula of the skull after traversing two layers of hypodermis: first, the layer lining the mandibular pocket, and second, the superficial layer of the head; in Anurida, however, I have found no such union between stirrup and skull. The body of the mandible is simply a modified cone, and hence in sections across this region appears as a complete chitinous ring (Plate **7**, Figures 44, 45, *md.*).

In Anurida no trace of a mandibular palpus exists at any stage, and, unlike Orchesella, no molar surface is differentiated; the latter fact is correlated with the character of the food: Orchesella feeds upon lignified vegetable substances, Anurida upon the soft tissues of the mollusk Littorina littoria. In further correlation with diet, the powerful rotators, or grinding muscles, of Orchesella are not represented in Anurida.

Several writers on Collembola have already given surface views of the mandibular fundaments at early stages, although none have traced their development. I refer especially to Lemoine ('**83**, Smynthurus) and Wheeler ('**93**, p. 57, Figure VI., Anurida). Packard ('**71**, p. 17; Plate **3**, Figure 13) evidently overlooked the mandibular fundaments of Isotoma, and what he regarded as mandibles are clearly, from their position, the first maxillæ. Ryder ('**86**) made the same mistake.

Claypole ('**98**, Plate XXIII.) gives several figures of the mandibular fundaments of Anurida maritima before much differentiation has occurred, and Uzel ('**98**, Taf. VI., Figur 87) represents the fundaments in Macrotoma (Tomocerus) at a stage equivalent to that of my Figure

21. He also gives a figure (Taf. V., Figur 64) supporting his statement (p. 22) concerning the appearance of the mandibular segments: "Ausserdem [collection of entoderm cells, etc.] bemerkt man zwei Paar dunkler Stelle, welche an den Ecken eines gedachten Quadrats sich befinden. Das dem Dorsalorgane genäherte Paar dieser Blastodermverdickungen (*kl.*) sind die getrennten Anlagen der Kopflappen, das zweite Paar (*mds.*) stellt die getrennten Anlagen des Mandibularsegmentes vor." The eggs of Anurida at my disposal were either too old or too young to show the condition here described by Uzel, although I did find a stage in which three pairs of fundaments were present, the third pair being the first maxillæ. The mandibles probably follow the procephalic lobes in appearance, as I have found all the stages necessary to indicate that the remaining paired appendages, except those of the superlinguæ, as I shall term them, appear successively from in front backward.

Campodea is structurally nearest to the Collembola, and, thanks to Uzel ('**98**, Taf. III., Figuren 35, 36; Taf. VI., Figuren 77–85), something is known concerning the development of its mouth-parts. The mandibular fundaments of Campodea are simple papillæ, as in Collembola; this simplicity distinguishes the Apterygota from the most generalized Pterygota, the Orthoptera, in which the fundaments are sometimes lobed.

The finished mandible of Campodea is strikingly like that of the Collembola, and is, moreover, of great morphological interest, because the structural correspondence of the mandible with the maxilla of hexapods — obscure in almost all other insects — is here a matter of direct observation, not merely one of inference. The mandible of Campodea (Meinert, '**65**, Taf. XIV., Figuren 15, 16; Nassonow, '**87**, p. 33, Figur 27) consists of a hollow fulcrum (stipes) and a head, which is separated from the fulcrum by a transverse suture. The head is composed of two parts, — a large, toothed, immovable, outer lobe or galea, and a smaller, fringed, movable, inner lobe, representing the lacinia.

Accepting the homologies with the first maxillæ implied in these terms, the palpus remains to be accounted for. A mandibular palpus has never been found among adult insects, — the evidence given for one by Hollis ('**72**) being quite vague and inadequate. Although the detailed development of the mouth-parts of Campodea has never been followed, it is in this most generalized insect that one may most hopefully look for a trace of a mandibular palpus, and we may safely predict that, if found, it will be a lateral, distal lobe of the stipal region, just as it is in the maxillæ of all insects.

The agreement between the finished mandibles of Campodea and Japyx, on the one hand, and Collembola, as represented by Anurida and Orchesella, on the other hand, is remarkably close. In both groups the mandible is hollow, has an oblique basal opening, which is large in Campodea, and, instead of an ordinary articulation, a free basal pivot, which is peculiar to the Apterygota. The homologies extend further, for I find that the similar and complicated movements of the mandibles are actually effected by muscles which are probably homologous in the two groups. The equivalence of certain muscles in Campodea, as represented by Meinert ('65, Taf. XIV., Figure 15) with others figured by myself for Orchesella (Folsom, '99, Plate 2, Figures 14, 15) may be expressed in tabular form as follows: —

Campodea (Meinert).			*Orchesella* (Folsom).
Muscle *C* (distal)	corresponds with		*9. add.*
" *C* (proximal)	"	"	*1. rot. l.*
" *D*	"	"	*5. pr't. l.* and *6. pr't. ms.*
" *E*	"	"	*3. ret. rot.* and *4. ret.*, or else *7. rot.* and *8. rot.*

The incompleteness of Meinert's figure prevents as exact a comparison as is desirable.

Japyx is nearest Campodea in structure, and the mandibles of Japyx, which have been described and figured by Meinert ('65), Grassi ('86^b), and v. Stummer-Traunfels ('91), are essentially like those of Campodea, but lack the articulated lacinial lobe, there being a lacinial region, however, which (Grassi, '86^b, Taf. II., Figura 14) is separated by a transverse line from the fulcrum. The muscles of Japyx agree with those of Campodea, and it is to be noted that the adductors originate upon a median chitinous plate, or tentorium, just as in Collembola, but not as in Orthoptera. The muscle *f* of Meinert ('65, Taf. XIV., Figuren 5, 15) has no homologue, it should be said, among the mandibular muscles of Orchesella, and I should be disposed to regard it as an adductor of the head of the first maxilla, had not v. Stummer-Traunfels ('91, Taf. I., Figuren 1, 3) figured the tendon of the same muscle in Campodea and Japyx going to the mandible. This author ('91, p. 220) erroneously states that the adductors of Collembola, Campodea, and Japyx are attached to the "Stützapparate," by which he means the lingual stalks (Plate 6, Figure 38, *pd.*^{1}); these, however, are quite distinct from the tentorium, which he apparently overlooked.

Nearly allied to the entognathous genera Campodea and Japyx are the ectognathous genera Lepisma and Machilis. In Lepisma the early development of the mandibles, as shown by Heymons ('**97**^{a}, Taf. XXX., Figuren 13, 15, 17, 20), is simple, and agrees with that of Anurida and Campodea. The finished mandible of Machilis (Oudemans, '**88**, Plate II., Figuren 25, 26), especially, recalls that of Campodea and Collembola by its elongated hollow fulcrum, oblique aperture, basal pivot, distinct head, and (as in Orchesella) well-developed molar surface; moreover, the adductors originate on a tentorium and are inserted within the mandibles (Oudemans, '**88**, Taf. **1**, Figur 19; Wood-Mason, '**79**, p. 148, Figure 1). Wood-Mason named the apex of the mandible "exopodite" and the molar lobe "endopodite," but upon superficial grounds, if one may judge from the evidence of embryology. Both lobes may together represent the endopodite; but the exopodite, or palpus, is unrepresented in the mandible, and it is a secondary lobe of the primary, or stipal, fundament, in the first and second maxillæ. Wood-Mason ('**79**) pointed out many interesting similarities which Machilis and Lepisma bear to the most generalized Orthopteran family, the Blattidæ, and remarked (p. 149), concerning the pivot of Machilis, that "the posterior ball-shaped condyle of mandibulated insects, clearly foreshadowed in the myriapod, is here fully formed and provided with a distinct neck."

The mandibles of Lepisma, however, more closely approach the Orthopteran type in being compact (v. Stummer-Traunfels, '**91**, Taf. II., Figuren 5, 6) and partly solidified, and in having broad incisive teeth, a molar surface like that of Orthoptera, and broadly attached adductors. The muscles are said by Oudemans ('**88**, p. 187) to resemble those of Machilis. V. Stummer-Traunfels represents the adductors only, and it may well be that the muscles are really much fewer than in Campodea and Collembola, such a reduction in number, if it occurs, being an approach to the Orthopteran type, in which but two mandibular muscles exist — a stout adductor and a slender abductor.

As to the development of the mandibles in Orthoptera, very little has been published. Ayers ('**84**, p. 241, Plate 18, Figures 20–22) says that in Œcanthus "the three oral appendages are trilobed; the lobation is most prominent in the second maxillary and least in the mandibular appendage. The primitive appendage is first divided into two lobes, and the inner of these becomes secondarily divided into two." The three lobes doubtless represent palpus, galea, and lacinia. Korotneff ('**85**, Taf. XXIX., Figure 6) figures lobed mandibular fundaments for Gryllotalpa. In other Orthoptera such lobation has not been recorded. In Blatta, according to Wheeler ('**89**, p. 348), "There are apparently no traces of lobation in the mandibles." Packard ('**83**^{1}, p. 279) says, "The mandibles [of Caloptenus] remain single-lobed," and both Wheeler ('93) and Heymons ('95^b) represent them as simple papillæ in all families of Orthoptera. It may at least be said, however, that the mandibles of Collembola and Thysanura are certainly homologous in their entirety with those of Orthoptera, and hence of all other insects.

It is an interesting fact that Heymons ('96, Taf. II., Figur 29) distinctly represents mandibular palpi for the larva of Ephemera, — a rare condition; indeed, Packard ('98, p. 61) terms this appendage of nymphal Ephemerids a "lacinia-like" process, although Heymons states (p. 21) that it is lateral in position, and so figures it.

What embryological evidence there is, then, confirms the view based upon anatomical data, that "the mandibles are primarily three-lobed appendages like the maxillæ" (Packard, '98, p. 61).

Turning now to the Myriopoda, the Symphyla, represented by the single genus Scolopendrella, show marked affinities with Campodea, as is well known. I wish here to emphasize especially the correspondences between the mouth-parts of the two genera, which have never been carefully compared in these respects.

Latzel ('84, p. 8, Taf. I., Figur 5) describes the mandibles of Scolopendrella as follows: "Die Oberkiefer bestehen jederseits aus einer fast horizontal gelagerten, trapezoidalen Chitinplatte, welche am End- oder Kaurande durch eine mittlere Einbuchtung in zwei Partien abgetheilt erscheint, von denen die vordere in vier kräftige, die hintere in vier bis fünf kleinere Zähnchen eingeschnitten ist. Eingelenkt sind diese Kieferplatten mit dem hinteren und äusseren Eck in eine zwischen Kopfdecke und Unterseite eingelagerte seitliche Lamina, welche einige Aehnlichkeit hat mit der Wange der Insecten und die von Menge als Theil (Stamm) der Oberkiefer aufgefasst wird. Am inneren Hintereck jeder der beiden Oberkieferplatten entspringt eine sehr kräftige Sehne, die in eine beträchtliche Anzahl von Muskelbündeln ausläuft, welche sich unten am Kopfrahmen inseriren."

The mandibles of Scolopendrella therefore resemble those of Campodea rather than those of any other insect, in that they are hollow, with a basal (stipal) part articulated to the skull, and a head separated transversely from the fulcrum. The head consists of two primary lobes (galea and lacinia) as in Campodea, but both are movable by muscles, whereas in Campodea the lacinia alone is articulated, and even this no longer has muscular attachments. The tendon and muscles which move the lacinia of Scolopendrella are exactly similar in position and function to the "chitinous rod" and muscles which adduct the head of the first maxilla of Orchesella, Japyx (Meinert, '**65**, Taf. XIV., Figur 8) and doubtless Campodea. More important, however, is the fact that the tendon of Scolopendrella is comparable with the mandibular retractor (cf. Latzel, '**84**, Taf. 1, Figur 5, ϵ, and Meinert, '**65**, Taf. XIV., Figuren 5, 15, *f.*, *flexor*) of Campodea and Japyx, and may be homologous with it. It can be easily understood that, if the terminal lobes in Scolopendrella became immovable by solidification in the mandible, the adductors of those lobes would then serve as retractors of the entire mandible, as in Campodea and Japyx.

Grassi ('**86**^{a}, pp. 15–16, Tav. II., Figure 2, 5) supplements Latzel's account of Scolopendrella by saying that no true cardo is present, and that the mandible is capable of lateral movements only.

Packard ('**83**^{b}, p. 198) says, "The so-called mandibles of the Myriopods are the morphological equivalents of those of insects, but structurally they are not homologous with them, but rather resemble the lacinia of the hexapodous maxilla." With the last assertion I do not agree. The mandibles of the more generalized Diplopods are in detail strikingly like those of Scolopendrella (Latzel, '**84**, Taf. I., Figur 5); for example, those of Polyzonium (Latzel, '**84**, Taf. XVI., Figur 203), in which the only fundamental difference is the presence of a cardo in Polyzonium, the stipes, galea, lacinia, and tendon being essentially as in Scolopendrella. The mandible, or protomala (Metschnikoff, '**75**), of Polyzonium does, indeed, resemble, not the lacinia, but the entire first maxilla of Thysanura and Collembola. The similarity, however, should not be mistaken for homology; it rather serves to emphasize the structural agreement of mandibles and maxillæ, — an agreement which gradually becomes obscure in the insect series through the progressive solidification of the mandible, but may nevertheless be traced, as I have shown, from Diplopoda and Symphyla, through Campodea and Japyx, Machilis and Lepisma, to the more generalized Orthoptera; thus the differences between the mandibles of Diplopods and Insects are not so great as Packard has affirmed ('**98**, p. 12).

The most that is known about the development of Diplopod mouthparts we owe to Metschnikoff ('**74**), who represents only two pairs of oral fundaments, designated "mandibles" and "labium." Although this conclusion is also reached by vom Rath ('**86**), I would not infer with Packard ('**83**^{b}, p. 199) that there can be only two pairs of oral appendages, but would suggest that embryological studies upon the mouthparts of other Diplopoda may, perhaps, show more.

The mandibles, or protomalæ, of Chilopoda are generally recognized as equivalent to those of Chilognatha, and, indeed, to the mandibles of Hexapoda and Crustacea. In the mandibles of Scolopendra (Meinert, '83, Taf. II., Figur 9), for example, there can be recognized cardo and stipes, a distinct head with galeal and lacinial lobes, and even muscles exactly comparable with the adductors and retractors of the mandible in Campodea and Japyx. The affinities of the Chilopods are, however, with the Diplopods, — from the stem-form of which they may have developed, — rather than with the Campodeidæ. Although Packard ('98, p. 15) states, "In the Chilopoda also the parts of the head, except the epicranium, are not homologous with those of insects, neither are the mouth-parts," there is really much indirect evidence of homology with the mouth-parts of insects through Diplopoda, Symphyla, and Thysanura, as is indicated above.

The mandibles of Crustacea have usually been considered homologous with those of insects. In Malacostraca (Reichenbach, '86), as in insects, the mandibular fundaments are a pair of appendages of the fourth primitive segment. In insects the exopodite (palpus) is absent, but in such generalized groups as Campodea and certain Ephemeridæ, a "lacinia mobilis" is present; in Malacostraca the palpus is present, and likewise, according to Hansen, a similar lacinia is found in the groups Mysida, Cumacea, Isopoda, and Amphipoda, although not in Decapoda.

Among insects, the Thysanura most nearly approach Crustacea. Hansen ('93, pp. 205–206) says of Machilis: "Die Mandibeln sind homolog mit denen der Malacostraken ; in Form sind sie denen der Cumaceen ähnlich, mit einer gut entwickelten, fast cylindrischen Pars molaris, doch ohne Lacinia mobilis; in Einlenkung und Musculatur stimmen sie erstaunend überein mit z. B. *Diastylis* und *Nebalia*." Referring to Campodea, Japyx, and Collembola, he remarks (pp. 208–209), "Die Musculatur der Mandibeln ist noch mehr der Crustaceen ähnlich als der Musculatur der *Machilis*. Vergleiche Meinert's Figur von *Japyx* mit meiner Figur von *Diastylis Goodsiri* in 'Dijmphna-Togtet' (ich habe nur die drei grössten Muskeln oder ihre Sehnen wiedergegeben) oder mit Sars' Figur von *Diastylis sculpta*, und man wird betroffen von der erstaunlichen Uebereinstimmung in Form und Richtung der Muskeln und der grossen medianen Muskelplatte."

In conclusion, the mandibles of Apterygota agree in development with those of Orthoptera, but show no trace of lobation except in Campodea, the most primitive form. The mandibles and maxillæ are homodynamous, and the former are homologous with the mandibles of Scolopendrella, Crustacea, and probably Diplopoda.

Lingua and Superlinguæ.

Not until Stage 3 are the fundaments of the superlinguæ ("paraglossæ" of some authors) observed; then a ventral aspect of the germ band (Plate 3, Figure 11) reveals two small papillæ (*su'lng.*) between the mandibles with their centres slightly more anterior than those of the mandibles. Although each small papilla is adjacent or contiguous to the mandibular fundament of the same side, it originates quite independently; in other words, it is not the inner branch of a biramous appendage, but a distinct ectodermal evagination, as transections of the germ band (Plate 4, Figure 23, *su'lng.*) prove.

At Stage 4 (Plate 3, Fig. 12, *su'lng.*) the superlingual fundaments are longer and stouter than before, and have moved back slightly in relation to the mandibles until nearly opposite them.

At Stage 5 the centres of the superlinguæ (Plate 3, Figure 21, *su' lng.*) are behind those of the mandibles, and in cross-sections (Plate 4, Figure 23) the former structures are seen to have exceeded the latter in rate of elongation. The long axes of the superlinguæ now diverge anteriorly from the median plane and the apices are partly under the mandibles, as in the adult, though the bases retain nearly their original positions in relation to the bases of the mandibles. During this stage is seen the first trace of the lingua (the "ligula," or "hypopharynx" of some authors), as a slight, median, unpaired, oval, ectodermal evagination (Plate 3, Figure 21, *lng.*) between the first maxillæ. This is the last of the oral fundaments to make its appearance.

In Stages 6 and 7 the lingua becomes longer and stouter, and, as seen in a ventral view of the germ band (Plate 5, Figure 30, *lng.*), its cross-section is rounded-triangular with its anterior median angle intruding between the two superlinguæ. Sections show that the lingua and superlinguæ have swung forward from their former positions at right angles to the germ band, and that the lingual and superlingual cavities are separately confluent with the general body cavity of the head. In the region of confluence a common cavity — a prolongation of the body cavity — is formed by a median evagination of the germ band itself. In Apterygota the superlinguæ, however, never become appendages of the lingua.

In ventral aspect, the lingua at Stage 7 (Plate 4, Figure 27; Plate 5, Figure 29) is cuneate with rounded apex, and, a little later (Plate 4, Figure 25, *lng.*) becomes constricted distally, forming a terminal lobe.

In Stage 8 the lateral surfaces (Plate 5, Figure 34) become concave, to correspond with the adjacent convex surfaces of the first maxillæ, as in the adult (Plate **7**, Figures 44, 45, *cht.*), and each ventro-lateral edge extends under the neighboring maxilla; in addition, the apex of the lingua becomes separated into two lateral lobes by a median sinus, and the dorsal surface invaginates to form a median longitudinal groove (Plate **7**, Figure 42, *sul.*) ; this lobed condition, however, is quite secondary in origin.

The lingua is thickly chitinized, and the hypodermal cells persist in the mature organ. The superlinguæ, on the contrary, are but thinly chitinized and at maturity contain no distinct hypodermis cells, except basally, although a complete layer of cells exists in Stage 8. In this stage (8) the superlinguæ become triangular in cross-section, as in the adult (Plate **7**, Figure 44). Partly on account of the divergence of the superlinguæ in front, but principally owing to the convergence of the mandibles and maxillæ, the attenuated distal part of each superlingua becomes situated between the apices of the mandible and the first maxilla of the same side (Figure 44), and the superlinguæ conform to the adjacent surfaces of the maxillæ.

The most interesting lingual structures are the two basal stalks (Plate **6**, Figure 38, *pd.'*), each of which articulates with the cardo of the same side and also furnishes a firm origin for the adductors and retractors of the first maxilla, as in Orchesella (Folsom, '**99**, Plate **3**, Figure 21). The development of these stalks has never been described. Although difficult to comprehend with a knowledge of the finished condition only, it is simpler than might be expected. The key to the understanding of its origin is the fact that each chitinous stalk is formed in a groove which is but a longitudinal evagination of the maxillary pocket, and follows the mesal surface of the first maxilla back to the cardo. The base of the lingual fundament is at *ba.* in Figure 30 (Plate **5**), and that of the maxilla at *ba.'* ; consequently the stalk is developed in a superficial groove of the germ band itself — that part of the germ band connecting the base of the lingua with the extreme base of the maxilla. In ventral aspect at Stage 7 (Plate **5**, Figure 29, *pd.'*), the continuity of the stalk along the surface of the maxillary pocket is evident. Dorsal to the stalk, of course, the base of the maxilla is connected with the head, but under the connecting region passes the stalk.

I must now explain how maxillary muscles become attached to the stalk in spite of the fact that the latter is a superficial formation of the hypodermis. This may be learned from transections at Stages 7 and 8, but also, and more easily, from good serial sections of an adult head, such as are shown in Plate **7**, Figures 46–50, which successively represent sections in more posterior planes.

Figure 46 shows the right maxilla (*mx.*^{1}) sectioned in front of its basal opening and lying free in its pharyngeal pocket; it also shows the stout, superficial chitinous stalk (*pd.*$'$) in its hypodermal groove. Figure 47 represents the beginning of an evagination (*pli.*) of the dorsal wall of the pocket, which grows down between the maxilla and chitinous stalk. Passing back, the intruding hypodermal fold expands, as in Figures 48 and 49 (*pli.*), until it almost encloses the stalk. Finally, in the region of the maxillary aperture (Figure 50), and on account of its obliquity, adductor muscles (*mu.*) are enabled to pass directly from the inner wall of the stipes to the chitinous stalk (*pd.*$'$). They are not attached directly to the stalk, but to an intervening cuticula (*cta.*); this, however, amounts to the same thing, because the cuticula and stalk become fused together at about Stage 7, and hardened into a single piece. It should be stated that the hypodermal cells which formed the intervening cuticula, as well as those which formed the stipes, are seen in embryological life only; they disappear at the origin and insertion of muscles.

At Stage 7 the end of each stalk is already feebly fused with the end of the cardo to form an articulation (compare Plate **4**, Figure 25, with Plate **6**, Figure 38, *atc.*). This is a simple process, as both cardo and stipes are superficial and contiguous structures. In the adult Orchesella (Folsom, '**99**, Plate **2**, Figure 10, *lig.*$'$) a long ligament unites them, and I mentioned a distinct suture as possibly indicating the end-to-end union of two ligaments, which doubtless occurred.

The lingual stalks, then, are quite independent of the lingua in origin, except that they are thickened cuticular structures continuous with the lateral cuticula (Plate **7**, Figure 45, *cht.*) of the lingua. When dissecting out the lingua at Stage 7, it frequently breaks away from the stalks at the sutures (*sut.*) shown in Plate **4**, Figure 25; these sutures later become obliterated, however.

The lingual stalks of Collembola have been mentioned by several authors, for example, de Olfers ('**62**, p. 18) in several genera, Tullberg ('**72**, Taf. IV., Figur 17) in Tomocerus, and v. Stummer-Traunfels ('**91**, Taf. I. Figur 7) in Tetrodontophora. I have seen them myself in all the more common genera; they undergo but little modification within the order.

As to the development of the lingua and superlinguæ in other insects, very little has been written. Packard ('**71**, p. 17), as quoted on page

128, did not find the "second maxillæ" (superlinguæ) in the embryo of Isotoma. Uzel alone has mentioned the embryonic lingua and superlinguæ of Apterygota. In Taf. VI. Fig. 87, he shows, in Tomocerus, three fundaments, which undoubtedly are these structures.

In Campodea, happily, Uzel describes with some detail the development of the "hypopharynx" (**'98**, p. 35): "Schon in jenem Stadium, bei welchem der Keimstreif sich in seinen mittleren Theilen in das Innere des Dotters einzusenken anfängt (Taf. IV. Figur 39), bemerken wir zwischen den beiden Anlagen der Mandibeln zwei einander sehr genäherte, ziemlich grosse, flache Platten (*hmd.*). Diese werden im nächsten Stadium, in dem die Umrollung des Keimstreifs vollendet ist, viel kleiner (Taf. VI. Figur 81, *hmd.*); dafür wölben sie sich jedoch bedeutend zu zwei spitzigen Höckern vor. Bald erscheint zwischen den Anlagen der ersten Maxillen eine unpaare, grosse, flache Platte (Figur 82, $hmx._1$), vor der man eine kleinere sieht. Letztere befindet sich zwischen den beiden vorher beschriebenen spitzigen Höckern und gehört noch dem Mandibularsegmente an (Figure 83, *hmd.'*). Die unpaare, dem ersten Maxillarsegmente angehörende Platte schickt sich nun an, über die beiden Höcker und die zwischen denselben gelegene kleine Platte vorzuwachsen (Figur 84), und zwar etwa in der Zeit, zu welcher das Thier ausschlüpft." After hatching, continues Uzel (**'98**, p. 48), "Von den drei schon früher beschriebenen Höckern, die zwischen den beiden Anlagen der Mandibeln lagen, wird der mittlere immer kleiner. Bei dem erwachsenden Thiere haben sich die beiden seitlichen zu runden bewimperten Schuppen umgebildet, welche von Meinert (**'67**) als Paraglossæ bezeichnet worden sind. Zwischen denselben befindet sich der nun sehr klein gewordene mittlere Höcker als unbedeutendes Gebilde, welches die beiden seitlichen Schuppen verbindet. Die grössere, zwischen den beiden Anlagen der ersten Maxillen gelegene Platte hat sich auch in eine, aber entsprechend der mächtigeren Anlage, grössere Schuppe verwandelt und ist über die beiden Schuppen des Mandibularsegmentes erst beim geschlechtsreifen Thiere gänzlich vorgewachsen (Taf. VI. Figure 85, $hmx._1$). Sie stellt Meinerts Ligula vor. Sowohl die von Meinert (**'67**) als Paraglossæ, als auch die von demselben als Ligula gedeuteten Theile sind, wie wir gesehen haben, ihrer Anlage nach als Hypopharynx aufzufassen."

The "hypopharynx" of Campodea is, then, undoubtedly homologous with the lingua and superlinguæ of Anurida, with the development of which it fundamentally agrees. In Anurida, however, as contrasted with Campodea, the superlingual fundaments do not show the early decrease in size, and a small median lobe does not appear on the anterior surface of the lingua.

In the finished condition in Campodea (Meinert, **'65**, Taf. XIV. Figuren 17, 19) lingua and superlinguæ are simple but distinct lobes, and the small fourth lobe mentioned by Uzel persists. The lingual stalks are surprisingly like those of Orchesella; the articulation with the cardo Meinert did not show, but it has since been observed by v. Stummer-Traunfels.

The English translator of Meinert's paper is really responsible for the use of the terms "lingua" and "paraglossæ" in connection with this subject, and not Meinert himself; the latter writer applied only the Danish expressions "Tungen" and "Bitungens tvende Flige."

Von Stummer-Traunfels (**'91**, Taf. I. Figur 11) also represents the "Ligula," "Paraglossæ," and "Stützstücken" of Campodea. On page 121 I criticise this author for holding that the so-called maxillary palpus of Collembola belongs to the neighboring superlingua. The embryology shows that the delicate membrane connecting either palpus and superlingua is of quite subsidiary importance, being simply as much of the cuticula of the maxillary pocket as intervenes between the base of a superlingua and the adjacent maxilla, — in fact, only the anterior portion of the cuticula surrounding the tissues which attach the maxilla to the head.

Japyx agrees closely with Campodea in the structure of these organs (Meinert, **'65**, Taf. XIV. Figur 8; von Stummer-Traunfels, **'91**, Taf. I. Figur 10), and there is no doubt about the homology of the lingua, superlinguæ, and lingual stalks of Japyx with those of Collembola. In the words of v. Stummer-Traunfels (**'91**, p. 221), "Diese typische Form des Stützapparates und der Befestigung der Cardines an diesem findet sich bei Campodea, Japyx und den Collembola in beinahe identischer Weise ausgebildet." The author is mistaken (**'91**, p. 222), however, in saying that the mandibles are attached to the Stützapparate, apparently having overlooked the tentorium, which is quite another structure than his "Stützapparat."

Regarding Lepisma, Heymons (**'97**^{a}, p. 595) simply remarks: "Ich . . . bemerke nur, dass die Bildung der einzelnen Körpertheile, z. B. des Hypopharynx der Mundwerkzeuge, durchaus an den bei Orthopteren bekannten Typus anschliesst."

Machilis, also, has decided Orthopteran affinities, as Wood-Mason (**'79**) found, yet the mouth-parts of both Lepisma and Machilis, although ectognathous, as in Orthoptera, are constructed upon fundamentally the same plan as those of the entognathous Apterygota. The similarity is evident in part from the following account of Machilis by Oudemans (**'88**, p. 186): "Letztere [Ligula], Figur 28 *Li*, reicht mit ihrem freien Ende ungefähr ebensoweit als die Unterlippe und wird durch zwei Chitinstäbchen gestützt, Figur 28 S, Figur 30 S. Mit der Ligula sind noch zwei Stücke, Figur 30 P, verbunden, die ich als Paraglossæ auffassen möchte. Sie sitzen an einer Chitinleiste, die sich auf der Dorsalseite der Ligula findet. Jede Paraglossa ist an ihrem freien Ende noch einigermassen vertheilt (ich glaube in drei Lobi) und hat einen kleinen Vorsprung an ihrer Basis, Figur 30 A. Es scheint mir, dass die Paraglossæ ausserdem noch festsitzen an den Stützstückchen der Ligula, Figur 30 S."

. . . "Die Maxillarspitzen treffen einander mithin in dem Zwischenraum zwischen Ligula und Paraglossæ, Figur 21, die Mandibularspitzen zwischen Paraglossæ und Labrum."

Von Stummer-Traunfels (**'91**) repeats some of Oudemans' figures of Machilis.

In Machilis, I find that the first maxillæ articulate with the skull — no longer with the lingual stalks — and the stalks, although evident, are much reduced and apparently functionless. The salivary glands open, as in Orthoptera, under the base of the lingua.

In Orthoptera, the most generalized of the Pterygota, there is a well-developed hypopharynx, or lingua, which exactly corresponds in position with the lingua of Apterygota, being a median papilla between the bases of the first and second maxillæ. In Periplaneta (Miall and Denny, **'86**, p. 127, Figure 71) it is borne upon two chitinous stalks, clearly comparable with those in Apterygota. Looking for traces of superlinguæ in Melanoplus femoratus, I found them, as large dorso-lateral rounded lobes, intimately united, however, with the lingua. This union is already foreshadowed in Machilis and Lepisma. I also found — almost accidentally — two rudimentary, chitinous, divergent stalks, extending back into the head from the ventro-lateral regions of the base of the lingua. The significance of these facts is clear, although the meaning of the lingual appendages, which have apparently been overlooked or disregarded in most Orthoptera, could hardly have been ascertained without studying the less specialized Apterygota. In Packard's figure of Anabrus (**'98**, p. 73, Figure 71), also, the lingua and left superlingua are evident.

In the rare and singular Hemimerus, Hansen (**'94**, pp. 70–71, Plate **2**, Figures 9, 10, *h.*) finds a "hypopharynx" and "maxillulæ," as well as chitinous stalks, all of which distinctly are as in Collembola, Campodea, and Japyx, except that the superlinguæ of Hemimerus appear to be fused with the lingua. Figure 10 of Hansen bears a close resemblance to my Figure 27 of Anurida, although Hansen says (p. 87), "especially the structure of the mouth removes it [Hemimerus] very far [?] from the Thysanura and leads it to the Orthoptera."

In the young larva of Ephemera, Heymons ('96, p. 22, Taf. II. Figur 29) finds that "Der Hypopharynx entsteht . . . auf ähnliche Weise wie bei den Orthopteren. Auch an ihm findet eine Art Gliederung statt, dergestalt, dass von der eigentlichen Hauptmasse zwei laterale vordere Zapfen abgetrennt werden, die mit kleinen Härchen bedeckt sind, während der eigentliche Hypopharynx am Ende einen Besatz von feinen (Sinnes-) Borsten trägt." His figure of lingua and superlinguæ might fairly represent those structures of Anurida in Stage 7 (Plate 4, Figure 27). In the imago the mouth-parts are, of course, atrophied. In another Ephemerid nymph, Heptagenia, Vayssière ('82, pp. 113–114, Planche 5, Figure 46) found a highly developed lingua, or hypopharynx, fused with large lateral pieces [superlinguæ] and suggests that they indicate a distinct primitive segment, — a possibility which will be discussed later. He states (p. 106), "La langue ou hypopharynx . . . est assez dévelopé chez tous les individus de la famille des Éphémérines, à l'exception du Prosopistoma, où il est très rudimentaire."

I shall not cite descriptions of the "hypopharynx" of additional insects, because I have nothing more to add, and the subject has been well treated of by Kolbe ('90, pp. 213–217, Figuren 126–134), Packard ('98, pp. 70–83, Figures 70–87), and others. Packard's comparative account, in particular, is most excellent and well illustrated. (In his Figure 69, by the way, the abbreviations *p.* and *hyp.* should be interchanged.) Briefly, the lingua is found in every order of insects, and although highly specialized in suctorial orders, retains, nevertheless, the same position and nearly the same relations to the salivary ducts that it does in the more generalized mandibulate orders which I have described. It is an interesting fact that in the Lepidopterous genus, Micropteryx, Walter ('85, Taf. XXIV. Figur 11) shows two hypopharyngeal stalks, readily comparable with those of Apterygota.

The superlinguæ — which, as I have shown, originate quite independently of the lingua in Apterygota, but become more or less united with it in Orthoptera and Ephemerida — should hereafter be recognized as morphologically important structures, and be searched for in even the most specialized haustellate orders as more or less intimate constituents of the "hypopharynx," which term, then, may refer collectively to the lingua and "superlinguæ." The necessity for this new term, also brought out on page 132, will appear from the following synonymical table: —

AUTHOR.	APTERYGOTA.	HYPOPHARYNX.	
		Lingua.	*Superlinguæ.*
De Olfers, '62	Collembola	lingua	organa cochleariformia
Meinert, '65	Thysanura	tungen	bitungens tvende Flige
" (trans.), '67	Thysanura	lingua	paraglossæ
Packard, '71	Collembola	. . .	second maxillæ
Tullberg, '72	Collembola	lamina hypopharyngis inferior	laminæ hypopharyngis superiores
Lubbock, '73	Collembola and Thysanura	ligula, lingua	second maxillæ
Grassi, '86	Thysanura	ligula	paraglossæ
Oudemans, '88	Thysanura	ligula	paraglossæ
V. Stummer-Traunfels, '91	Collembola and Thysanura	ligula	paraglossæ
Hansen, '93	Collembola and Thysanura	hypopharynx	maxillulæ
Heymons, '97	Lepisma	hypopharynx	
Uzel, '98	Collembola and Thysanura	hypopharynx	
Folsom, '99	Collembola	glossa	paraglossæ

Among Pterygota, the term "hypopharynx" of Savigny is fixed in application, although the compound nature of the organ is not generally known. Synonymous with "hypopharynx" are the following terms (see also Packard, **'98**, p. 71): lingua (Savigny, **'16**), ligula (Kirby and Spence, **'28**), langue ou languette (Dugès, **'32**), lingua (Westwood, **'39**, p. 9), tongue (Taschenberg, **'79**), hypopharynx (Dimmock, **'81**; Burgess, **'80**, and most others).

"Ligula," "glossa," and "paraglossæ" are terms established in Pterygota, but less fixed in the little-known Apterygota, and therefore more easily discarded in the latter group, as advised on pp. 132–133. "Maxillulæ" and "second maxillæ" as applied to superlinguæ are unfortunate because based upon unproved homological assumptions. The need for a new term, then, becomes evident. I have therefore suggested "*superlinguæ.*"

In Scolopendrella authors have omitted to mention whether the hypopharynx is present or not.

Referring to Diplopoda, however, to which Scolopendrella is most nearly related, Packard (**'98**, p. 13) says, "The hypopharynx, our 'labiella' (Figure 6), with the supporting rods, or *stili linguales* (*sti. l.*), of Meinert, are of nearly the same shape as in some insects." Latzel (Taf. IX. Figur 104; Taf. VI. Figur 72) represents "ein Zwischenstück der

Zunge," for Lysiopetalum and Craspedosoma respectively, as well as two lateral lobes, or "Zungenlappen" (lobi linguales). These structures, although united with the gnathochilarium, are probably homologous with the separated lingua and superlinguæ of Apterygota, but, in the absence of the necessary embryological investigations, that is all that may be said.

In the Chilopoda no structure analogous to the hypopharynx appears to be known.

The "superlinguæ" of insects are homologous with the first maxillæ of Crustacea. In Anurida I have found (Plate **4**, Figure 28, *su'lng.*) a distinct primitive ganglion — the fifth — for the superlinguæ, representing the fifth, or first maxillary, ganglion of decapod Crustacea. This ganglion is eventually incorporated with the subœsophageal ganglion, and no superlingual nerves develop. Moreover, the superlinguæ originate between the mandibles and so-called "first maxillæ" of Anurida. The superlingual fundaments, however, never become biramous — an exopodite or palpus does not appear — and are not segmented, like the Crustacean first maxillæ. In fact, they are much reduced structurally and functionally in Apterygota, and gradually reduced to disappearance in ascending the Pterygote scale.

Hansen (**'93**) regarded the superlinguæ — or "maxillulæ," as he termed them — from their position, as equivalent to the Crustacean first maxillæ, emphasizing the opinion of v. Stummer-Traunfels (**'91**) that the superlinguæ bore palpi. The latter argument cannot be used, however, because, as I show (p. 121), the palpi in question belong to the "first maxillæ."

The lingua, usually termed "hypopharynx" among insects, may easily be homologized with the hypopharynx of Malacostraca. It originates quite independently of the superlinguæ as a median, unpaired papilla, is not supplied with a primitive ganglion or distinct nerves, and can no more be regarded as a distinct segment than can the labrum. In Orchesella and Anurida it finally becomes distinctly bilobed by a median groove, but the bilateral condition is clearly secondary. Packard's evidence (**'98**, pp. 82–83) that the hypopharynx is "composed of, or supported by, two bilaterally symmetrical styles both in Myriapods and in insects" has little weight, in view of what I have found to be the development of these "lingual stalks."

The hypopharynx of insects, then, is a compound structure, the components of which originate independently. The median ventral lingua, like the labrum, does not represent a pair of appendages; the dorso-lateral "superlinguæ," which have been usually overlooked or disregarded in Pterygote insects, represent a distinct though reduced somite, as confirmed by the presence of a primitive ganglion. The superlinguæ are homologous with the first maxillæ of Malacostraca, and are probably represented in Diplopoda.

The lingua of insects is homologous with the Crustacean hypopharynx and probably with the median constituent of the gnathochilarium of Diplopoda.

Maxillæ.

The fundaments of the "first maxillæ" appear next after those of the mandibles, and at Stage 1 (Plate **1**, Figure 1 ; Plate **2**, Figures 8, 8a, *mx.*^{1}) are a pair of small hemispherical papillæ, similar to those of the mandibles. At Stage 3 they are longer than the mandibles and must consequently have lengthened faster. As seen in transections of the germ band, the maxilla is at first a simple ectodermal evagination, apically rounded, but at Stage 3 (Plate **3**, Figure 15) the apex is flattened, and a lateral lobe, the beginning of the palp, has appeared ; this lobe is also seen in the ventral aspect of the germ band (Plate **3**, Figure 11, *plp.*) as well as in the lateral views (Plate **2**, Figures 9, 10). The posterior aspect of the left first maxilla when dissected out is given in Plate **3**, Figure 17.

At Stage 4 (Plate **3**, Figures 12, 19) the maxilla has elongated considerably and its base is covered by the lateral fold of the germ band (Plate **3**, Figure 19, *pli. or.*), as already mentioned. In the following stage (Plate **3**, Figures 20, 21, *mx.*^{1}) the maxilla and palpus, though longer, are more nearly concealed by the lateral fold. The form of the maxilla with its palpus at this stage is shown in Figure 22, which was drawn from a dissection ; the base of the maxillary fundament is already oblique, precisely as described for the mandibles, and the first maxillæ have begun to converge toward the median plane. It is to be remembered that the palpus is here a secondary lobe of the primary fundament.

At Stage 7 (Plate **4**, Figure 24 ; Plate **5**, Figures 29, 30, *mx.*^{1}) the first maxillæ, now covered by the lateral folds, have swung forward through an angle of almost ninety degrees (Figure 24), like the mandibles. Claypole ('**98**, p. 263) states that "a flexure of the embryo begins that results in crowding the mouth-parts together to form a definite head," but such a purely mechanical interpretation will not serve, because the paired mouth-parts are still at right angles to the germ band long after involution has occurred (Stage 5, Figures 5, 20). During this stage (7) the first maxillæ are attenuated toward their free ends; a ventral view (Plate 5, Figure 29, *mx.*[1]) shows their position in relation to the lingua, and the extent of their convergence toward each other. The maxilla is quite unattached to the pharyngeal pocket (Plate 7, Figures 44–50, *cav. buc.*) in which it lies, except where the margin of its basal aperture becomes confluent with the wall of the pocket (Figure 50); it has the form of a modified cone with an oblique, dorso-mesal, basal opening, as shown in transections (Figures 44–50, *mx.*[1]). The parts named *stipes* and *chitinous rod* in my paper upon Orchesella are, as I have since found in that genus and in Anurida, distinguished simply by a greater deposition of chitin, and are connected above and below by delicate chitinized membranes, which I did not recognize until influenced by embryology to search for them. The "chitinous rod," then, is proved both by anatomy and development to be but a part of the stipes.

During this stage (7) certain important differentiations of the first maxillæ are observable, if those organs are dissected out. The articulation between stipes and cardo (Plate 6, Figure 38, *atc.*) appears superficially as a notch, and in frontal section as a less chitinized region, as might be expected; in a small hypodermal pocket is formed the stipal projection (Figure 38, *prj.*) noticeable in the finished organ. The cardo, now transverse in position, was formerly the basal region of the lateral surface of the primary maxillary fundament, before the basal attachment became oblique. The articulation between the cardo and lingual stalk was described on page 112.

In this stage, too, the head of the maxilla becomes vaguely separated from the stipes by a constriction (Plate 5, Figure 29). Later, the constriction is more pronounced (Plate 4, Figure 25), and the apex of the head is fashioned into an acute curving lobe, — the fundament of the galea (Plate 4, Figure 26, *ga.*) or "aussere Lade." The "head" is lined with a continuous layer of hypodermis cells. Next, on the mesal side of the head, a second lobe appears, the lacinia (*lcn.*), or "innere Lade." Both galea and lacinia, then, become toothed on the mesal face, the teeth of the latter being produced each by a single cell; the larger teeth of the former are secreted each by many cells. Eventually (Plate 6, Figure 39) the galea (*ga.*) becomes thickly chitinized except for a central hollow core, but the lacinia (*lcn.*) remains thinly chitinized even in the adult. As in the mandibles, the hypodermis is finally excluded from the head of the maxilla, but through an opening in the constricted region nerve fibres may be traced to the lacinia.

At this stage (7) the first maxillary palpus (Plate **5**, Figure 30, *plp.*), though still present, is no larger than it was in Stage 5 (Figure 22, *plp.*). In the newly hatched insect no trace of this palpus exists, hence it must have been resorbed. In the adult Orchesella, on the contrary, the palpus is functional and highly developed; other facts also indicate that Anurida is a degraded form.

Von Stummer-Traunfels (**'91**, p. 226, Taf. I. Figuren 6, 7), following Tullberg (**'72**, Taf. IV. Figur 17), observed a connection between the maxillary palpi and the so-called paraglossæ of Collembola, and makes use of this union (p. 226) as the first of his reasons for recommending an improved designation of the mouth-parts, in the following words: "I. Die grosse Unwahrscheinlichkeit, dass der sogenannte Maxillartaster der Collembolen wirklich zur Maxille gehört, indem diese von jenem vollständig getrennt ist und derselbe vielmehr in innigem Verbande mit den Paraglossen steht." Hansen (**'93**, p. 209) uses this conclusion in proving that the "paraglossæ" of Collembola and Thysanura are homologous with the first maxillæ of Crustacea. Without discrediting his conclusion, I have already shown (Folsom, **'99**) upon anatomical data the trivial nature of the union between palpus and "paraglossæ" (superlinguæ). I have now proved upon embryological evidence (Plate **3**, Figure 22) that the palpus belongs to the maxilla, and have also shown (p. 114) that the chitinous membrane connecting it with the superlingua is simply incidental, and is only that part of the wall of the maxillary pocket which necessarily intervenes between the first maxilla and superlingua of the same side.

The fundament in Isotoma designated first maxilla by Packard (**'71**, Plate **3**, Figure 13) is undoubtedly, from its position in relation to the first pair of legs, second maxilla; therefore what he regards in the same figure as a mandible must be a first maxilla. Ryder (**'86**) followed Packard in this matter, but Wheeler (**'93**, p. 57, Figure 6) shows the fundaments in their proper position.

Claypole (**'98**) correctly identifies the first maxillary fundaments in Figures 43, 46, and 47, but does not mention the palpus.

Uzel (**'98**) gives a figure of the first maxillary fundaments of Tomocerus and remarks (p. 36): "In jenem Stadium, bei welchem die Umrollung des Keimstreifs vollendet ist, bemerken wir, dass sich die Anlagen des ersten Maxillenpaares (Taf. VI. Figur 87, $mx._1$) in zwei Höcker getheilt haben, und zwar in einen äusseren länglichen und in einen inneren stumpf dreieckigen. Der innere Höcker dürfte nach Analogie mit Campodea den lobus internus, der aüssere die gemeinschaftliche Anlage des Lobus externus und des Palpus maxillaris vorstellen." I entirely disagree with the author as to the interpretation of the lobes. In Anurida the lobus externus is not developed out of the palpal lobe of the biramous fundament, but the remaining lobe is the common fundament of lobus externus and lobus internus. Therefore Uzel's foot-note on page 36, "An den Maxillarpalpen von Macrotoma (Tomocerus) vulgaris fand ich selbst einen kleinen Vorsprung, der wohl als Lobus externus zu deuten ist," etc., is open to criticism; the minute papilla to which he refers is precisely like several other papillæ distributed upon the palpus (see Folsom, '99, Plate 3, Figure 18, *plp.*), except for a trifling difference in size. It is very doubtful if a difference in this matter exists between Anurida and Tomocerus, especially since the process as observed by me agrees with that of insects in general, as far as is known, excepting possibly Lepisma, presently to be noticed.

Uzel applied to Tomocerus conclusions drawn from Campodea, in which he ('98, pp. 33–34, Taf. VI. Figuren 79, 80) derives the galea from the palpal lobe. His diagrams, unfortunately, do not elucidate the basal relations of the three principal lobes: palpus, galea, and lacinia.

The completed first maxillæ of Campodea (Meinert, '65, Taf. XIV. Figuren 17, 18; Grassi, '86^b, Tav. IV. Figure 2, 13; v. Stummer-Traunfels, '91, Taf. I. Figuren 5, 11) are remarkably like those of Collembola (Folsom, '99, Plate 3, Figures 18–21): the cardo is articulated to the superlingual stalk in the same way; the hollow stipes, distinct head, galea, and lacinia are also alike, and resemble less the homologous parts of Pterygote insects. The solid bifid galea and the fringed seven-lobed lacinia of Campodea, as I call them, are by Grassi and v. Stummer-Traunfels regarded collectively as the "innere Lade" or lacinia. The latter author says (p. 223), "Man kann daher bei den drei vorliegenden Formen eine successive Rückbildung des Aussenladens annehmen. Bei *Japyx* noch zweifach gegliedert, ist er bei Campodea schon mehr reducirt und fehlt bei den Collembolen gänzlich." It is curious to observe how authors have followed one another in deriving the galea from the palpal fundament. I have shown in Anurida (anticipating later conclusions) that the galea and lacinia both originate from the "endopodite" of the bifid fundament.

Japyx, of course, agrees substantially with Campodea. The second maxilla, however (Meinert, '65, Taf. XIV. Figuren 8, 9; Grassi, '86^b, Tav. II. Figure 2, 3, 6, 8; v. Stummer-Traunfels, '91, Taf. I. Figuren 4, 10) has a two-lobed galea and a four-lobed lacinia.

In Japyx, thanks to Meinert's figure ('65, Taf. XIV. Figur 8), the muscles may be clearly homologized with those I ('99, Plate 3, Figures 20, 21) have described for Orchesella. As Meinert did not designate the muscles, I can simply say that they severally correspond with those labelled by me *3. add.*, *4. add.*, *10. add.*, *7. add.* or *9. pr't. add.*, and one muscle with both *5. pr't. add.* and *6. pr't. add.*, while one of two others probably represents *8. ret. add.*

In Lepisma, according to Heymons ('97ᵃ, p. 592, Taf. XXX. Figuren 13, 15, 17, 20), the fundament of the first maxilla forms the palpus, at the base of which appears a mesal lobe, which itself divides to form galea and lacinia. This account is, then, at variance with mine on Anurida, that of Uzel on Campodea, and that of Ayers for the Orthopteran genus Œcanthus, and is, so far as I know, unsupported by the results of other authors. In fact, Figure 13 of Heymons even suggests that the palpus is a lateral lobe of the primary fundament, as I have found it to be in Anurida. As to the origin of the three first maxillary lobes, Uzel, Heymons, and myself disagree, as I have said. Uzel's account agrees with mine, in so far as he makes the palpus a lateral evagination of the primary, or stipal, fundament; and Heymons, like myself, derives both lacinia and galea from the inner lobe of a biramous appendage.

In its final form, the first maxilla of Lepisma is easily recognized as homologous with that of other Thysanura, but approaches remarkably the same organ in Orthoptera, especially that of the Blattidæ. As in other Apterygota, the stipes (v. Stummer-Traunfels, '91, Taf. II. Figur 11; Muhr, '77, Taf. VII. Figur 45) has a basal opening, cardo, distinct head, galea, and lacinia, and the origin of the muscles (Oudemans, '88, p. 187) "findet man auch hier an Chitinstücken im Kopfe." The palpus in Lepisma, however, is five-jointed, as in Orthoptera. What I call galea and lacinia are also, in this particular case, named "Aussenlade" and "Innenlade" by v. Stummer-Traunfels.

Machilis is nearer than Lepisma to Campodea and Collembola in the structure of the first maxillæ. As may be seen from the figures by Oudemans ('88, Taf. II. Figur 27) and v. Stummer-Traunfels ('91, Taf. II. Figuren 8, 9, 10), the positions of the cardo, stipes, galea, lacinia, and palpus are exactly comparable in the three groups. The palpi in Machilis, to be sure, are seven-jointed, and a palpiger is present, as in Orthoptera. The structure identified by v. Stummer-Traunfels as

"Aussenlade" in Machilis, cannot be homologous with the part bearing the same name in other insects, for in Machilis it is clearly a part of the palpiger instead of being a constituent of the head of the maxilla. The two adductor muscles described by Oudemans ('**88**, Taf. I. Figur 19) as extending from the inner wall of the maxilla to a median tentorium, are probably the homologues of *5.* and *6. pr't. add.* of Orchesella (Folsom, '**99**, Plate **3**, Figure 20).

In Œcanthus, Ayers ('**84**, p. 241, Plate **18**, Figures 20–22; Plate **19**, Figure 5) has traced the development of the first and second maxillæ as far as the trilobed condition, his ideas (p. 241) agreeing with mine on Anurida: "The primitive appendage is first divided into two lobes, and the inner of these becomes secondarily divided into two." Patten ('**84**, p. 596) says, "A rather striking variation was found in the first and second maxillæ of Blatta, which were formed respectively of two and three lobes." Wheeler ('**89**, p. 348) adds, regarding the same genus, "The outer of the three lobes of each maxilla becomes the palp, while the inner two become the galea and lacinia of the adult." Heymons ('**95**^{b}, p. 19) states that in Forficula, "drei selbständige Aeste zu erkennen sind, aus denen Lobus internus (lacinia), Lobus externus (galea) sowie der Palpus hervorgehen." This trilobed stage is exactly comparable with that of Lepisma, although Heymons and Ayers differ as to its derivation.

Although Wood-Mason ('**79**) emphasizes the agreement between Machilis and Orthoptera, I may say that Lepisma is intermediate between the two in structure, with decidedly orthopteran affinities. Especially is this true of the first maxillæ. The cardo, stipes, galea, lacinia, and palpus of Lepisma (Muhr, '**77**, Taf. VII. Figur 45, or v. Stummer-Traunfels, '**91**, Taf. II. Figur 11) not only agree in position with those of Blatta (Muhr, '**77**, Taf. II. Figur 12, or Packard, '**83**^{a}, Plate XXVIII. Figure 12, Periplaneta), but exhibit a surprising agreement in form, as well as the number of palpal segments; in both groups, also, a palpifer is differentiated. Through Lepisma, therefore, the first maxillæ of Collembola may be homologized with those of Orthoptera, and hence all other Pterygote orders. I have traced the homologies, part for part, between Lepisma and all the families of Orthoptera, as well as the genera Ephemera, Myrmeleon, and Corydalus, in which latter genera the nymphal first maxillæ are but little specialized in form. Heymons ('**96**, p. 19) states that in the Libellulid genus Epitheca, "Erst später gliedert sich von der Aussenseite der Maxille eine kleine rundliche Erhebung ab, welche die Anlage des Tasters darstellt (Figur

19, *palp. mx.*[1]), während das in der directen Fortsetzung des ursprünglichen Maxillen-Zapfens liegende Endstück zur Lade (lobus) wird." This agrees with Anurida, Campodea, and Œcanthus, but disagrees with the account given by Heymons himself for Lepisma.

Turning to the Myriopods, Scolopendrella, while undoubtedly more closely allied to the Diplopods, nevertheless shows in many ways interesting correspondences with Campodea, as other writers have already stated. The lateral parts of the plate termed the "gnathochilarium" resemble in several respects the first maxillæ of Campodea. According to Latzel (**'84**, Taf. I. Figuren 6, 7) and Grassi (**'86**[a], Tav. II. Figure 5, 10), there is an elongated hollow stipes bearing an outer (galeal) and also an inner (lacinial) terminal lobe, both of which agree in detail with the comparable structures of Campodea and Japyx; for in Campodea, a one-jointed palpus is present, and in Campodea, Japyx, and Collembola, a "chitinous rod" extends backward from the lacinia. The few muscles shown by Latzel (**'84**, Taf. I. Figur 7) are to be compared with *5.* and *6. pr't. add.*, and *8. ret. add.* of Orchesella (Folsom, **'99**, Plate **3**, Figures 20, 21). Grassi (**'86**[a], p. 16) states that muscles from within the organ pass to an endoskeleton, which, as one may see from his Figure 25, is essentially like the "lingual stalks" that I have found in Orchesella and Anurida, and still more nearly like the same structure of Campodea and Japyx. All these similarities confirm the view, based primarily upon other anatomical data, that Scolopendrella most clearly represents the hypothetical ancestor of insects.

Among Diplopods the passage from the more generalized genera, as Lysiopetalum or Craspedosoma, to Scolopendrella is clear. In the first genus, especially, are seen a cardo (not described as yet for Scolopendrella), stipes, galea, and lacinia, all simple in structure, but no palpus. I should state, however, that it remains to confirm these homologies by embryology.

In Campodea the second pair of jaws is usually homologized with the first maxillæ of Insects; but, except in position, there is little resemblance between the two organs.

The first maxillæ of insects are usually homologized with the first maxillæ of Crustacea, but if, as I maintain, the "superlinguæ" are equivalent to the latter organs, it follows that the hexapod first maxillæ correspond to the Crustacean second maxillæ.

The primitive biramous character of Crustacean mouth-parts is well known, and Hansen (**'93**, p. 198) has, in connection with this subject, formulated a significant law — "dass man drei Glieder im Stamm von allen gespalteten Gliedmassen bei den Crustaceen als ein primäres Verhältniss annehmen muss, und diese Zahl hat sich, wenigstens in den angeführten Fällen, deutlich erhalten." In fact, Hansen himself (p. 206) has homologized the first maxillæ of Machilis with the second maxillæ of Crustacea, on account of the three axial segments and the position of the palpus, saying: "Der Bau der Maxillen . . . stimmt also genau mit den Maxillen der Eumalacostraken."

The axial segments of the Crustacean appendage are on this view successively equivalent to cardo, stipes, and palpifer of Hexapoda.

It must be admitted that these anatomical agreements, if appealed to alone, may logically be used to support other views than my own, since all the Crustacean appendages are constructed upon the same plan; but the equivalence of the neuromeres in Hexapoda and Crustacea is a matter of the greatest significance. Viallanes has proved that the first three neuromeres in the two groups agree in great detail, and I find that his conclusions apply equally well to the succeeding neuromeres. It is very significant that in most cases the appendages of equivalent somites have the same function in the two groups, and that all the paired nerves of the head in Collembola agree exactly in position with those of decapod Crustacea.

Summarizing: The first maxillæ of Apterygota develop in all essential respects like those of Orthoptera, with which they may be homologized in detail. In Anurida a palpus appears, but is resorbed before hatching, indicating the descent of Anurida from a form in which the first maxillary palpi were functional. The first maxillæ of Campodea are clearly to be homologized with those of Scolopendrella, and less clearly with the lateral portions of the Diplopod gnathochilarium. The first maxillæ of Hexapoda pass through a biramous stage, such as obtains among Crustacea, are comparable with Crustacean second maxillæ in some detail, and are homologous with those of Malacostraca.

Labium.

The fundaments of the labium, or "second maxillæ," appear next after those of the first maxillæ, and at Stage 1 (Plate **1**, Figure 1; Plate **2**, Figure 8, *mx.*^{2}) are a pair of simple conical elevations rising perpendicularly from the germ band and slightly longer than the fundaments of the mandibles and first maxillæ. In the following stage (2) they are longer and more cylindrical (Figure 2); in Stage 3 (Figure 3) they are somewhat larger, and ventral or lateral surface views of the germ band (Plate **2**, Figures 9, 10; Plate **3**, Figure 11) disclose a distinct lateral lobe, the palpus (*plp.*), which is larger than that of the first maxilla. A second maxilla, as dissected out at this stage, is shown in Figure 18 (Plate **3**). Transections of the germ band (Plate **3**, Figure 14) show the palpus to be an outfolding of the antero-lateral face of the primary maxillary evagination, just as in the case of the first maxilla.

At this stage (Plate **2**, Figures 9, 10) there appears near the mandibles a lateral evagination (*pli. or.*) of the germ band, destined to form the side of the face; this fold grows backward until it involves the base of the second maxilla of the same side, and the internal cavities of the two folds become one. In Stage 4 (Figure 4; Plate **3**, Figure 19) it has already involved the base of the second maxilla; the apex of the maxilla, however, is still free from the fold, and the palpus (Plate **3**, Figure 12, *plp.*) is as large as that of the first maxilla.

At Stage 5 the second maxillæ (Figure 5; Plate **3**, Figure 20, *mx.*^{2}) are long, oval in cross-section, and project at right angles to the germ band; the antero-lateral region of the base is confluent with the mouth-fold (Figure 21). At this period all trace of the second maxillary palpus becomes lost; it has not become involved in the mouth-fold, which is still restricted to the base of the maxilla, but has been rapidly resorbed and appears at last as indicated in Figure 20. In the next stage (6) the second maxillæ (Figure 6) converge toward the median plane like the other pairs of oral organs, and similarly swing forward.

At Stage 7 (Plate **2**, Figure 7) the second maxillæ and mouth-folds are quite confluent (Plate **5**, Figures 30, 34), but the anterior part of each maxilla is still distinguishable as a swollen lobe, or less flattened region (Plate **4**, Figure 24, *lab.*). The bases of the second maxillæ, although widely separated in Stage 5 (Plate **3**, Figure 21, *mx.*^{2}), subsequently spread toward the median plane, become thinner, and gradually form a single plate; the median sinus between them shortens until the condition shown in Plate **5**, Figure 29 (*lab.*) is attained. The union of the second maxillæ with each other is not a simple contact and fusion resulting in a median suture; but a confluence of the cavities of the two maxillæ occurs and progresses forward (*i. e.*, distally), ceasing, however, before obliterating the median sinus, which remains in the adult (Plate **7**, Figures 43, 45, *sut. m.* and *sul.*). Although the finished labium bears a median ventral groove, the groove does not indicate the fusion of the fundaments; at Stage 7, when the labial plate is complete, no trace exists of the groove, which is formed in a later stage. A comparison of my figures (Plate 3, Figure 20; Plate 5, Figure 29) will show that practically the entire ventral surface of the head is labial in origin, because the original bases of the second maxillæ extended quite to the first pair of legs; an inconsiderable, if any, portion of the germ band intervening (Figure 21) between them.

At Stage 8 the mouth is nearly closed (Plate 5, Figure 34) by the overgrowth of the combined second maxillæ and mouth-folds.

In the adult (Plate 7, Figure 43) the apical lobes, although in contact mesally and stoutly chitinized, are readily separable and may be depressed and elevated by muscles homologous with those of Orchesella, the hinge lines being shown at *sut.* Shortly before hatching, hypodermis cells evaginate singly to form the external setæ of the head.

In the development of the labium, as I have traced it, neither galea nor lacinia becomes differentiated; but the terminal lobe is equivalent to the head of the first maxilla, and therefore represents the common fundament of galea and lacinia, the second maxilla not passing the biramous stage. All of the labium behind the terminal lobe represents not only the stipes and cardo of the first maxilla, but also the mentum, submentum, and gula of the Orthopteran labium, — an important conclusion.

In Orchesella (Folsom, '99, Plate 3, Figure 24) mentum, submentum, and gula appear to be indicated, but the development in Anurida throws no light upon the structures which I suggested might be modified palpi.

Packard ('71, p. 17) in describing Isotoma says, "I was unable at this or any other period to discover any traces of the second maxillæ. Though existing in a very rudimentary state in the adult, I could not detect them after repeated attempts, but do not doubt but that a more skilled observer would have made them out. Indeed, it is a most difficult thing to discover their rudiments in the adult; I failed, at the time these observations were made, to detect them, though since then I have succeeded in making out their structure and relation to the surrounding parts of the mouth." As a matter of fact, he (Plate 3, Figure 13) has evidently figured the second maxillæ, which I know to be present in the genus, and in the passage quoted he doubtless referred to the superlinguæ ("paraglossæ"), which Lubbock also ('73, p. 66) termed "second maxillæ." Ryder ('86, Plate XV. Figures 7, 9, 10), too, repeated the mistake in Anurida.

Claypole ('98, Plate XXIII. Figures 40–44, 46, 47) represents the fundaments as simple papillæ without distinguishing the palpi, which are, however, obscurely indicated in Figures 43 and 47.

Uzel ('98, Taf. VI. Figur 87) shows the papillæ of the second maxillæ in Tomocerus. Concerning the development of the second maxillæ in Campodea, he ('98, p. 33) says, "Auch an den Anlagen der zweiten Maxillen (Taf. IV. Figur 38 und Taf. VI. Figur 79, $mx._2$) lässt sich ein kleinerer lateraler und ein grösserer medialer Theil unterscheiden, die indess nicht scharf von einander gesondert sind." . . . (p. 34) "An den Anlagen der zweiten Maxillen tritt auf der Mitte des Hinterrandes ein Vorsprung auf (Fig. 80, le_2), aus welchem sich, wie wir voraussenden wollen, der Lobus externus entwickelt, wogegen der früher besprochene innere Theil den Lobus internus (li_2) und der äussere den Palpus labialis (pmx_2) aus sich entstehen lässt. Zugleich bemerkt man an den beiden Maxillenpaaren eine gewisse Rotation. Die äusseren Enden derselben bewegen sich nämlich nach vorn (Fig. 80), so dass die beiden Anlagen eine schräge Stellung erhalten. Bald jedoch, und zwar in dem Stadium, wo die vollkommene Umrollung des Keimstreifs zustande gekommen ist (Fig. 41), kehren sie in die ursprüngliche Lage zurück (das erste Maxillenpaare nicht ganz), und es erfolgt nun eine Rotation des zweiten Maxillenpaares allein im entgegengesetzten Sinne; die äusseren Enden desselben bewegen sich nämlich jetzt nach hinten und drehen die ganze Anlage in eine entsprechende schräge Lage, welche aus Fig. 81 ersichtlich ist.

"Im nächsten Stadium (Fig. 82) . . . die Anlagen des zweiten Maxillenpaares haben eine dreilappige Gestalt angenommen. Die drei Lappen lassen sich leicht deuten, wenn man die vorhergehenden Stadien vergleicht. Der vorderste (li_2) entspricht dem Lobus internus, der mittlere (le_2) dem Lobus externus, und der hintere, breit gerundete (pmx_2) stellt den Palpus labialis vor. Auch bemerken wir, dass sich nach der erwähnten Rotation die beiden Anlagen des zweiten Maxillenpaares einander stark in der Medianlinie genähert haben (Fig. 82) und auch etwas nach vorn gerückt sind." "In den nächsten Stadien (Fig. 83 und 84), bei welchem der Keimstreif schon etwas spiralig gerollt erscheint (Fig. 42), rücken die Anlagen des zweiten Maxillenpaares noch näher aneinander, und zwar ganz besonders die Lobi interni (li_2)." In the postembryonic stage (p. 47): "Die beiden Anlagen des zweiten Maxillenpaares rücken in der Mittellinie noch näher als früher zusammen, so dass nicht nur die Lobi interni ($limx_2$), welche sehr gross geworden sind, sondern auch die Lobi externi ($lemx_2$) dicht neben einander zu liegen kommen. Eine Verwachsung der beiden Hälften des zweiten Maxillenpaares findet jedoch auch beim erwachsenen Thiere nicht statt."

It is not clear, then, whether the galea develops from the outer or the inner lobe of a biramous appendage, although Uzel's account is, at least, not inconsistent with his description of the first maxillæ, which I have already criticised. Although Uzel does not state as much, his figures indicate the palpus to be an appendage of the primary fundament, as it is in Anurida. In this genus, however, no third branch appears, as I have said; but, from analogy with the first maxilla, the inner of the two branches represents undifferentiated galea and lacinia.

The rotation in a frontal plane of the second maxillary fundament of Campodea — which does not occur in Anurida — enables me to homologize the finished labium of Campodea with the apparently different labium of all other insects. If Uzel's figures are compared with Figure 12 of v. Stummer-Traunfels (**'91**), it is easy to see that the embryonic structures by Uzel designated $limx_2$ (lacinia), $lemx_2$ (galea) and pmx_2 (palpus) are with hardly a doubt respectively represented in the adult by the parts which v. Stummer-Traunfels termed *up.* ("untere Mundplatte"), *pl.* ("tasterförmige Papille") and *pp.* ("Tastwarze"). These homologies, however, could never have been settled upon merely anatomical grounds.

What Grassi (**'86**^{b}, Tav. IV. Figura 3), then, considered to be the under lip (*la. in.*) of Campodea is but the anterior part of the true labium; the "labial palpi" (*pa. li.*) are really galeæ borne upon a region representing the mentum, and the "labial papillæ" (*pa. la.*) are but modified palpi. As in Collembola, the labium is anteriorly and deeply cleft.

Japyx is so close to Campodea that the same conclusions may doubtless be applied to both genera. In Japyx the labium, as in Collembola, is split and bears a median sulcus (Grassi, **86**^{b}, Tav. III. Figura 21) much like that of Orchesella (Folsom, **'99**, Plate **4**, Figure 29). Examining Figure 1 of v. Stummer-Traunfels (**'91**, Taf. II.), the lacinia and galea are clearly represented, as in Campodea; the true palpus, however, is but obscurely differentiated in the region behind the so-called palpus (*pl.*) and nearer the median plane. The eversible papillæ of the anterior part of the labium, as described by Meinert (**'67**, p. 369) and Grassi (**'86**^{b}, p. 31), are probably homologous with the papillæ of Orchesella which I designated *plp.* (**'99**, Plate **3**, Figure 24).

For Lepisma, Heymons (**97**^{a}, p. 590, Figur 11) gives, first, a pair of simple second maxillary fundaments and later (Taf. XXX., Figur 20) a long palpus with a small, basal, inner lobe, and states (p. 592) "Die Lobi oder späteren Ladentheile der Maxillen sind in diesen Stadien erst als sehr kleine unscheinbare Vorsprünge erkennbar, welche medialwarts an der Basis der Taster hervorwuchern." This is contrary to the conditions in Anurida, where the palpus is certainly itself an outgrowth from the simple, primary papilla (Figure 13). Lepisma agrees with Anurida, however, in that the galea and lacinia are derived from the inner lobe of a biramous fundament (Heymons,' **97**^{a}, Taf. XXX. Figur 17), and disagrees with Campodea if, in the latter genus, as Uzel implies, the galea buds from the palpus. The finished labium of Lepisma, as I shall show, is remarkably like that of Orthoptera.

The labium of Machilis, as described by Oudemans ('**88**, pp. 185–186, Taf. II. Figuren 28, 29), resembles that of Campodea and Collembola in being deeply cleft, and having the salivary ducts opening in similar positions, but it more nearly approaches the Orthopteran type in the position and structure of the terminal lobes, the mentum, and the three-jointed palpi. Each terminal lobe is subdivided into four lobes, which in all probability collectively represent galea and lacinia.

Ayers ('**84**, p. 241, Plate 18, Figures 20–22; Plate 19, Figure 5), as already quoted (p. 124), has traced the development of the second maxillæ of Œcanthus as far as the trilobed stage, stating the lobation to be more prominent in the second than in the first maxillary appendage. The fact that the second maxillæ of Anurida develop upon the Orthopteran type is important. In Lepisma, the trilobed fundaments agree with those of Orthoptera even as to the greater length of the palpus.

In the finished labium of Œcanthus (Packard, '**83**^{a}, Plate XXVII. Figure 9) the derivatives of each trilobed fundament are easily identified as three-jointed palpus, galea, lacinia, palpifer, and mentum, — the last two structures having doubtless arisen from the common stalk, or stipes. Although the labium is constructed upon the same plan in all Orthoptera, we may best select Blatta for comparison with Lepisma. The agreement between Blatta (Muhr, '**77**, Taf. II. Figur 11; Packard, '**83**^{a}, Plate XXVII. Figure 14) and Lepisma (Muhr, '**77**, Taf. VIII. Figur 46; v. Stummer-Traunfels, '**91**, Taf. II. Figur 17) is surprising. Galeæ and laciniæ clearly correspond in the two, as do the mentum, palpifers, and palpi, the last, however, having three segments in Blatta and four in Lepisma. Muhr, in fact, included Lepisma among Orthoptera, as have some other authors.

It is now agreed that the first and second maxillæ of Orthoptera are homodynamic, and, more inferentially, that the same is true of other insects. The exact agreement first recognized, according to Packard ('**98**, p. 69), by Miall and Denny ('**86**), was detected long before, at least, by

Muhr ('77, p. 9) and by Schaum ('61, p. 84). In Anurida the whole gular region, excepting the terminal lobes and palpi, represents the undifferentiated gula, submentum, mentum, and palpifers; therefore the gula in Orthoptera may be regarded as the united cardines, and the submentum, mentum, and palpifers, as stipal derivatives. It will be seen that my view differs from those accepted and defended by Packard ('98, p. 69) and others; but it is supported by embryological evidence, while the other views are not. It may safely be predicted that the apparently unpaired gula of Orthoptera will be shown to originate from paired fundaments, as I have found it to do in Anurida.

If these homologies between Collembola, Thysanura, and Orthoptera are accepted, their extension from the last group to other Pterygote orders is not difficult, even though the desirable embryological verifications are still wanting.

There is an unfortunate confusion of terminology regarding the mouth-parts of insects. The homologies are much obscured, but less by the use of different terms for homologous parts, than by the use of the same name for parts which are not homologous. "Paraglossæ" and "ligula" are cases in point. To most entomologists "paraglossæ" mean indifferently the labial lobes homodynamic with the galeæ and the laciniæ of the first maxillæ, or else mean the galeal lobes alone, while "ligula" or "glossa" signifies the lacinial lobes, often more or less fused into a median organ; in fact, "ligula" is often used synonymously with "labium" in reference to many Coleoptera (Le Conte and Horn, '83, p. xviii). "Ligula," however, is often made a synonym of "lingua" (Packard, '98, p. 68), and the latter term, of "hypopharynx." In my opinion, the term "lingua" should be restricted to the median, unpaired constituent of the hypopharynx; for the "hypopharynx" of certain insects often bears two dorso-lateral lobes which in more generalized insects are not only free from the lingua, but quite distinct from it in origin (as proved by myself in Anurida and by Uzel in Campodea), and these dorso-lateral appendages are most frequently called "paraglossæ," upon assumptions which are not sustained by embryology, as I shall presently show.

As the terms "paraglossæ" and "ligula," or "glossa," are irremovably fixed, as applied to labial structures, they should not be used for anything else. It is both unnecessary and impossible to displace the term "hypopharynx," but it is necessary to recognize the overlooked fact that the "hypopharynx" is frequently a compound organ, to the ventral and median component of which the term "lingua" may well be restricted; while, for the dorso-lateral appendages, rejecting "paraglossæ," I propose the more appropriate name "superlinguæ."

The "gnathochilarium" of Symphyla and Diplopoda may also prove to be in part homologous with the hexapod labium. Having already discussed the resemblances between the lateral portions of the gnathochilarium and the first maxillæ, I may compare the median components with the labium. They were, in fact, designated "under lip" in Scolopendrella by Grassi (**'86**^{a}, Tav. II. Figura 5). As in Apterygota, there is a median portion and two stipal plates, each of which bears a papillate head, separated by a transverse suture. These are the only points of agreement. On the contrary, the gnathochilarium is usually homologized with the first maxillæ of insects (Packard, **'83**^{b}, p. 199; Korschelt u. Heider, **'90-93**, p. 906) — apparently on account of Metschnikoff's (**'74**) researches. I can only suggest that the under lip of Diplopods is anatomically of too compound a nature to be homologized with the first maxillæ only, and that we are not warranted in deriving the entire lip from only two primary fundaments simply because Metschnikoff did not allude to more than two. In fact, Heymons (**'97**, p. 7, Figur 2) has discovered a "post-maxillary" segment, without appendages, in the embryo of Glomeris; but he regards it as equivalent to the labial segment of insects. In other Diplopoda, for example Lysiopetalum (Latzel, **'84**, Taf. IX. Figur 104) and Craspedosoma (Latzel, **'84**, Taf. VI. Figur 72), the structure of the under lip is remarkably like that in Scolopendrella.

In Chilopoda there are two fleshy, jointed appendages ("first maxillipedes," "zweites Unterkieferpaar"), which are conceivably equivalent, in position only, to the second maxillæ of Hexapoda, and are generally homologized with the first pair of legs of Diplopoda. If the second maxillæ of insects are represented among Diplopoda in the manner I have suggested, then the second pair of Chilopod "maxillipedes" ("Kieferfusspaar") corresponds with the first pair of feet of both Diplopoda and Hexapoda, — a simple conception.

The labium of Hexapods is homologous with the first pair of maxillipeds of Crustacea, according to the homologies which I have already proposed for all the more anterior paired appendages. It is, then, erroneous to homologize with each other the second maxillæ in these two classes; but the error is so firmly established that I have in this paper frequently employed the term "second maxillæ" for the labium of insects, in order to avoid confusion.

The evidence for my view of the homologies of the labium is of the same character as that already used for the "first maxillæ." The labial fundaments are appendages of the seventh somite in both Hexapods and Crustacea and are supplied by equivalent ganglia and nerves. In both groups each fundament is at first simple and secondarily develops a palpus, or exopodite. Moreover, the axis of the appendage is three-segmented, the segments in Crustacea corresponding to gula, mentum, and palpifers of generalized Hexapoda, the submentum being a secondary development.

Hansen ('**93**, p. 206) differs slightly: "Das Submentum [Machilis] ist mit dem, bei den Gammarinen zusammengeschmolzenen ersten Gliede homolog, das Mentum mit dem bei den Hyperinen auch zusammengeschmolzenen zweiten Gliede; auf der Spitze des Mentums findet man ein Glied, das auf jeder Seite in vier Laden ausgeht, die, wie sich ziemlich deutlich zeigt, zwei Laden angehören, die jede für sich gespalten ist, und diese halte ich (unter Anderem wegen eines Vergleiches mit Orthoptera und Amphipoda, kann aber keinen zwingenden Beweis von den Skelettheilen führen) respectiv für eine Lade vom zweiten Gliede (die innerste gespaltene Lade) und für das dritte Glied des Labiums mit seiner gespaltetem Lade; der Palpus geht von der Aussenseite des dritten Gliedes aus."

Hansen should have taken into consideration the gula, and the fact that the submentum is probably not a primitive sclerite.

The homologies between Hexapoda and Crustacea that I have defended are none the less valid if the total number of somites differs in the two classes, and they are sustained if the number is the same. In decapod Crustacea there are twenty-one somites, including the ocular segment. In generalized insects the number of abdominal segments varies. In the embryo of Lepisma, which shows marked affinities with Crustacea and Orthoptera, Heymons ('**97**^{a}) finds eleven abdominal somites. Add to these the thoracic segments and the seven which I have found in the Apterygote head; and the total, twenty-one, is the same as for decapod Crustacea. In embryos of many families of Orthoptera and Odonata just eleven abdominal segments are present. On the other hand, Heymons ('**95**^{b}) has found twelve in certain genera of the same orders, and in Collembola the number varies greatly. In view of this variability within the limits of the same order, then, it is well not to emphasize the agreement between generalized insects and decapod Crustacea in the total number of somites.

My conclusion regarding the labium, then, is that its development in Apterygota conforms to the Orthopteran type. In Anurida a labial palpus is formed and resorbed, — an indication of degeneracy. The entire gular region of Apterygota is labial in origin; but fewer sclerites are differentiated than in Pterygote insects. The labium of insects is homodynamous with the "first maxillæ" and homologous in detail with the first maxillipeds of decapod Crustacea. The labium of Campodea is equivalent to the "second maxillæ" of Symphyla, and is represented in the Diplopod gnathochilarium.

Skull.

The principal mouth-parts of Collembola, unlike those of all other insects, except certain Thysanura, are internal; the way in which they become so will now be described.

The beginning of the process is seen at Stage 3 (Plate **1**, Figure 3), when the ventral surface of the germ band is almost flat. In lateral aspect (Plate **2**, Figures 9, 10) the edge of the germ band is produced downward as a small crescentic lobe (*pli. or.*) outside the fundaments of the mouth-parts. This lobe usually originates on the mandibular segment, as represented in Figure 9, but may arise more anteriorly, as in Figure 10. These figures represent, respectively, the left and right sides of the same individual. Rarely, the lobe begins behind the mandible. A transection of the germ band near the middle of the lobe (Plate **3**, Figure 16) proves the lobe (*pli. or.*) to be an evagination of the ectoderm enclosing mesoderm. In ventral aspect at this stage (Figure 11) the mouth-fold is clearly distinguishable at its widest part, or place of origin, but gradually disappears anteriorly and posteriorly on account of its confluence with the rest of the germ band.

At Stage 4 (Plate **1**, Figure 4) and a little later, while involution of the germ band is occurring, the mouth-fold is considerably larger (Figures 12, 19, *pli. or.*) and forms a crescentic flap, now extending from the second maxilla almost to the labrum. In the next stage (Plate **1**, Figure 5) the fold is conspicuous; in lateral aspect (Plate **3**, Figure 20) its ventral margin is well rounded and conforms posteriorly to the contiguous anterior surface of the front leg; the mandibular and maxillary fundaments still project slightly below the fold. In ventral aspect (Plate **3**, Figure 21) of the same individual, the fold is seen to be of nearly uniform width except anteriorly and posteriorly, where it is expanded against the labrum and second maxillæ respectively. Transections of the germ band (Plate **4**, Figure 23), when compared with similar sections at Stage 3 (Plate **3**, Figure 16), show the folds to have exceeded the mandibles in rate of downward growth, and the lateral surface of the mandible to be concave, in conformity with the swollen distal region of the mouth-fold.

In Stages 6 and 7 (Plate **1**, Figure 6; Plate **2**, Figure 7) the folds involve the labrum and second maxillæ (Plate **4**, Figure 24; Plate **5**, Figure 30, *pli. or.*), covering the mandibles and first maxillæ laterally, and forming the genæ, or sides of the face. As seen in Stage 7 (Plate **5**, Figure 30), each oral fold connects one side of the clypeo-labral fold with the labial evagination of the same side. There are no sutures, however, to indicate the union of the genæ dorsally with the clypeus and ventrally with the second maxilla, for the oral evagination, in its backward and forward extension, has at length involved the labial and clypeal folds, respectively, in such a way that all three folds become one and enclose a single common cavity. The anterior margin of the mouth-fold is still distinguishable, however, as late as Stages 7 and 8 (Plate **4**, Figure 24, *pli. or.*); the mesal surfaces of the labial fundaments have not united anteriorly (Plate **5**, Figure 29); the labrum is free from the fold (Figure 30) and remains so. The mouth is definitely bounded, but still open (Figures 30, 34); its closure occurs, however, before the egg hatches. The folds — clypeo-labral, oral, and labial — have been converging concomitantly with their elongation, and continue to elongate and converge until they meet to form a buccal cone, which completely encloses the inner mouth-parts. After hatching, there is, for reasons just given, no demarcation of the mouth-fold; it can simply be said that the region designated as *pli. or.* in Figure 40 (Plate **6**) is the anterior part of that fold. Also in Orchesella the corresponding region, under which project the palpi (Folsom, '**99**, Plate **2**, Figure 9), doubtless originates as in Anurida, but the clypeus is not confluent with the folds.

Strictly speaking, then, the mandibles and maxillæ are *not* "retracted," as is usually stated; but they are overgrown by the genæ.

Hansen ('**93**, p. 208) wrote concerning Campodea, Japyx, and Collembola, "die Mandibeln und Maxillen, mit Ausnahme der Spitzen, 'im Kopfe liegen.' Dieses ist dadurch entstanden, dass sich die Haut hinter ihrer Einlenkung wie eine Duplicatur, welche Gewebe enthält, vorwärts und um sie herum gefaltet hat, und die Ränder dieser Duplicatur sind auf der Unterseite des Kopfes mit dem Seitenrändern des Labiums festgewachsen, so dass dieses fast seiner ganzen Länge nach mit der Seitenwand des Kopfes verbunden ist." These facts he ascertained by laborious dissections of the finished parts.

Packard ('**71**, p. 21) simply mentions that "the cephalic plates, which fold back upon the head, forming the main expansion of the insectean head is [are] apparently the tergum of the antennary segment," — a statement unsubstantiated by later and more extensive studies.

The only account of the formation of the mouth-folds of Collembola is by Miss Claypole, who also studied Anurida maritima, giving her results briefly in 1896 and finally in 1898. The following extracts from her valuable paper ('98, pp. 264–266) summarize her observations and conclusions: "On each side of these [three pairs of mouth-parts, as in my Stage 3] has appeared a ridge that passes backward along the embryo, the two folds enclosing the mandibles and maxillæ. These folds start from just the region where the small intercalary appendages were seen earlier, but which have now disappeared. Figures 43, 46, and 47 show the process by which this change takes place, and leave no doubt that the folds, as they finally appear, are a development from the intercalary appendages. . . . The labrum in front and these lateral folds make together a three-sided box in which the mouth-parts, two mandibles, and four maxillæ are sheltered. . . . The second pair of maxillæ has been modified to form the back of this pouch." The author (pp. 265–266), after homologizing the neuromeres of Orthoptera and Crustacea, draws the important conclusion that the mouth-folds of Anurida "including without doubt its allied forms," are "clearly homologous with the second antennæ" of Crustacea.

I quite disagree with this author as to the origin, and consequently the homology, of the mouth-folds. A priori arguments are here superfluous, as the question is one of fact. As I have shown, the folds begin on, or very near, the mandibular segment, but always outside the paired fundaments of the mouth-parts, and never at the premandibular appendages. The folds eventually and necessarily involve the intercalary region on progressing towards the labrum, although previously their early indicated continuity with the second maxillæ (Plate 2, Figure 10) is established. Conceptions as to the development of the fold are of course but inferences from facts observed in certain stages. The most apparent inference from the figures cited by Miss Claypole as leaving no doubt about the accuracy of her conclusion is certainly the one she has drawn; but from the same figures and from her preparations — which Miss Claypole has most kindly lent me — may also be drawn the less apparent, though I believe correct, inference that the folds begin between the intercalary and second maxillary regions and grow towards both of them. I have found stages intermediate between those shown by Miss Claypole in Figures 46 and 47, which convince me that this is the case. Consequently the mouth-folds cannot represent the Crustacean second antennæ. My own views as to the homology of the mouth-folds, already implied by my use of the term "genæ," will presently be supported.

Hansen's recognition of the similarity between Campodea, Japyx, and Collembola is sustained by embryology. In Campodea, Uzel ('98, p. 33) describes and figures a "Chitinstrang . . ., welcher sich von der Vorderrandmitte der zweiten Maxille um die Aussenseite des ersten Maxille und der Mandibel herum zu den auf den Intercalarsegmente gelegenen Höckern zieht." His Figures 38 and 79 show the Chitinstrang at a rather advanced stage of development, corresponding with the condition in my Figure 17; unfortunately he gives neither its origin nor its earlier development. The later development, as evidenced diagrammatically by his Figures 80–84, agrees with that of Anurida in the gradual approximation of the lateral ridges, and especially in the completion of the buccal boundary by the same method of confluence. Uzel does not attempt to explain the homology of the Chitinstrang.

In Lepisma and Machilis the mouth-parts are ectognathous, as in Orthoptera. In Lepisma there is no trace of a lateral mouth-fold, but in Machilis I have found a distinct, flat, lateral lobe sheltering the base of each mandible, and the lobe is probably homologous with the Collembolan mouth-fold.

In Pterygota the genæ, often not demarcated as distinct sclerites, represent the lateral regions of the germ band — as they do in Campodea and Collembola. In these Apterygota the same areas have simply increased as folds, but the folds are none the less homologous with the pleural regions of other insects, and in Collembola are reasonably to be regarded as the pleural portions of the premandibular, mandibular, and both maxillary segments. In many Pterygote insects, especially in Orthoptera, the genæ overlap the bases of the jaws; for example, in Caloptenus, in which the gena is produced as a small but distinct flat fold over the base of the mandible.

Little is known about the development of the sides of the head in Myriopoda, but in Peripatus it is interesting to find distinct lateral mouth-folds (Sedgwick, '88, Plate II., Figure 36) quite analogous, to say the least, with those of Collembola.

Concerning the completion of the skull, little remains to be said. At Stage 7 a constriction encircling the blastoderm separates the head from the thorax. The head is typically a hollow cylinder, or cone, and so is the body. The body cylinder consists of a definite number of successive rings, in each of which, in the more specialized insects, tergum, pleura, and sternum are present.

In the head region of the Collembola, however, segmentation occurs only on the ventral side of the germ band. The entire gular region is labial in origin, and there is reason for regarding the clypeus as the tergite of the ocular segment. The mouth-folds are undoubtedly expanded pleura. Aside from these, however, it is idle to speculate about the location of other sclerites which are differentiated in more specialized insects. Here, in the absence of such differentiation, it may be be said that the head-cylinder represents seven ideal rings, which dorsally and laterally are in no way demarcated from each other. Admitting that the procephalic lobes do extend backward and encroach upon other segments, the lobes may not be regarded as the tergites or pleurites of those segments, for they are simply thickened blastoderm, and increase in area in proportion as the blastoderm thickens; but the convenience of applying a single term, "procephalic lobe," to either of these thickenings should not blind us to the fact that the lobe eventually represents the blastoderm of more than one segment.

In the finished head (Plate 5, Figure 33) are certain elevated dorsal areas which, however, are not sclerites bounded by sutures, and are not clearly to be homologized with sclerites of other hexapod orders. The elevations referred to are directly correlated with underlying glands and muscles.

The sides of the face in Apterygota, then, are homologous with the genæ of Pterygota. In all insects the skull represents seven somites, but the cephalic sclerites of Pterygota, excepting labrum, clypeus, and labial sclerites, are not differentiated in the Apterygota.

Tentorium.

The tentorium of Anurida is essentially like that of Orchesella (Folsom, '99), consisting of a chitinous plate parallel with the frontal plane (Plate 8, Figure 51, *tnt.*), from which diverge two pairs of chitinous arms (Plate 6, Figure 35) extending to the skull: a dorsal pair (*br. d.*) and a posterior pair (*br. p.*) embracing respectively the supra- and infra-œsophageal ganglion. A third, or anterior, pair was found in Orchesella, but not in Anurida.

Regarding the development of the tentorium in insects, most diverse opinions are held. After considerable study, I have come to the conclusion that the tentorium of Anurida is derived from proliferated ectodermal cells which are in no way, except in position, distinguishable from young ganglion cells.

In Anurida, as in Orthoptera (Wheeler, '93, Heymons, '95[b]) and Lepisma (Heymons, 97[a]), the ventral cords consist of dorso-ventral rows of cells, which arise by proliferation from the outer ectoderm. Although it has seldom been supposed that these cells became other than ganglionic in function, it may be assumed, in view of their origin, that all of them are potentially chitin-forming cells, and it seems probable that some of them actually do form the chitinous tentorium.

An oblique section of Stage 8, cut at a fortunate angle for studying the relation of tentorium to cells, gave the appearance represented in Figure 35. Contiguous to practically all parts of the tentorium, in this section, are cells the nuclei of which do not differ in appearance from nuclei of undoubted ganglion cells. On all sides of the tentorium such cells abound and closely embrace it; an especially large mass of these cells occurs immediately under the frontal plate, in which, moreover, several cells always become enclosed and appear to be functional in the adult. I found no evidence which could be interpreted as indicating any other way of formation.

Von Stummer-Traunfels ('91) appears to have overlooked the tentorium of Apterygota, for he mentions the "Stützapparate" only, by which he evidently means the structures I call "lingual stalks."

As regards the Thysanura, Meinert ('65, Tab. XIV. Figur 5, *b*) mentions in Japyx and Campodea a median chitinous plate, from which the mandibular adductors take their origin, which is undoubtedly the tentorium. Grassi (86[b]) also alludes to it in Japyx.

In Machilis the lingual stalks, important in Collembola, become rudimentary; and most of the mandibular and maxillary muscles become attached to the tentorium; but they are fewer than in Collembola. The tentorium is thus described by Oudemans ('88, p. 186): "Die vorderen [Stützplatten] kommen von den Seiten des Clypeus, gleich oberhalb der Mahlhöhle, wie dieses im Durchschnitt abgebildet ist in Figur 32. Links und rechts geht dort die Chitinhaut des Clypeus über in eine Platte. Die beiden Platten nähern sich nach hinten, indem sie fortwährend breiter werden. In der Mitte des Kopfes kommen sie zusammen, sind da jedoch nicht verschmolzen, sondern nur stark durch Bindegewebe verbunden, Figur 19 L[1]. Hinter dieser Verbindungsstelle weichen die Platten wieder auseinander, werden schmäler und gehen, links und rechts vom Œsophagus, nach oben. Zuletzt geht jede über in einen dünnen Chitinstab, welcher oben im Kopfe, hinter den Augen, endet und da am Chitin des Kopfes festsitzt."

Thus, the tentorium of Machilis is constructed upon the same plan as that of Anurida, although the median plate is halved longitudinally. The dorsal and posterior arms in Anurida are clearly represented in Machilis, and the latter pair tends to become reduced in size, — an approach to the Orthopteran condition.

The tentorium in Orthoptera is readily comparable with that of Machilis. In Periplaneta, according to Miall and Denny (**'86**, p. 39), "In front it gives off two long crura, or props, which pass to the ginglymus, and are reflected thence upon the inner surface of the clypeus, ascending as high as the antennary socket, round which they form a kind of rim. Each crus is twisted, so that the front surface becomes first internal and then posterior as it passes towards the clypeus. The form of the tentorium is in other respects readily understood from the figure (Figure 17). Its lower surface is strengthened by a median keel which gives attachment to muscles. The œsophagus passes upwards between the anterior crura, the long flexor of the mandible lies on each side of the central plate; the supraœsophageal ganglion rests on the plate above, and the subœsophageal ganglion lies below it, the nerve-cords which unite the two passing through the circular aperture. A similar internal chitinous skeleton occurs in the heads of other Orthoptera, as well as in Neuroptera and Lepidoptera."

In Anabrus (Packard, **'98**, p. 49, Figure 33) the tentorium is essentially the same, with a central plate, and paired dorsal and posterior arms. The only important differences between Orthoptera and Collembola in respect to the tentorium are (1) that the œsophageal commissures pass through it in the former group instead of around it; (2) that in Orthoptera the posterior arms are reduced in length, and (3) that the tentorium becomes more stoutly chitinized. On the other hand, the tentorium of Orthoptera, in its general form and topographical relations, agrees closely with the same structure in Collembola and Thysanura.

Palmén (**'77**) derived the tentorium from a pair of cephalic tracheæ in Ephemera, but upon unsatisfactory grounds. In Collembola tracheæ are absent; moreover, as Packard (**'98**, p. 50) notes, "the apodemes of the thoracic region are evidently not modified tracheæ, since the stigmata and tracheæ are present."

The views of Carrière (**'90**) and Cholodkowsky (**'91**), agreeing with the opinion of Palmén, have been controverted by Heymons (**'95^b**, pp. 50–51).

Wheeler ('89, p. 568) finds that five pairs of ectodermal invaginations form the tentorium of the larval head of Doryphora. "These invaginations grow inwards as slender tubes, which anastomose in some places. Their lumina are ultimately filled with chitin." Wheeler offers his observations in support of Palmén's theory, but they are not at all inharmonious with the scanty observations I have made upon Anurida.

Heymons ('95^{b}, pp. 50–51), describing Forficula, agrees with Wheeler, except that he finds only two pairs of fundaments for the tentorium, and says (p. 51): "Ich habe mich indessen davon überzeugt, dass auch bei Gryllus und Periplaneta die zahl der Tentoriumanlagen keine grössere ist, sondern, wie Heider ('89) dies bei Hydrophilus beschrieb, und ich es bei Forficula fand, nur vier beträgt. Der oben geschilderte Entwickelungsmodus des Tentoriums dürfte daher wohl als der typische anzusehen sein."

In Anurida I was unable to find any distinct ectodermal invaginations which might form the arms of the tentorium, but am not prepared to say that none exist, because the subject is one of great difficulty. The arms must be studied in oblique sections, and it is almost impossible to distinguish them from fundaments of muscles until they are nearly completed. The finished tentorium of Collembola, however, is undoubtedly homologous with that of Thysanura, and almost as clearly with the tentorium of Orthoptera.

Segmentation of the Head.

The elucidation of the primitive segments in Arthropods is a most interesting and difficult morphological problem. The rule of Savigny, — emphasized by Huxley and others, — that Arthropods consist fundamentally of successive rings, each of which may bear but one pair of primary appendages, although now undoubted, has never been thoroughly substantiated when applied to the Hexapod head. After years of argument, morphologists still disagree as to the number of somites composing the highly differentiated heads of insects. Kolbe ('90, p. 135) recognizes five, as follows: —

1. Ursegment: Fühler, Augen, Oberlippe;
2. Ursegment: Oberkiefer oder Mandibeln (1. Kiefernpaar);
3. Ursegment: Unterkiefer oder Maxillen (2. Kiefernpaar);
4. Ursegment: Zunge oder Innenlippe (3. Kiefernpaar, verwachsen);
5. Ursegment: Unterlippe (4. Kiefernpaar, verwachsen).

Sharp ('95, p. 87) says, "Morphologists are not yet agreed as to their number, some thinking this is three, while others place it as high as seven; three or four being, perhaps, the figures at present most in favor, though Viallanes, who has recently discussed the subject, considers six, the number suggested by Huxley, as the most probable. Cholodkowsky is of a similar opinion."

Packard ('**98**, p. 54) gives six: —

	Name or Segment.	Pieces or Regions of the Head-Capsule.	Appendages, etc.
Pre-oral in early embryo.	1. Ocellar (Protocerebral).	Epicranium, anterior region with the clypeus, labrum, and epipharynx.	Compound and simple eyes (ocelli).
Post-oral in early embryo.	2. Antennal (Deutocerebral).	Epicranium, including the antennal sockets.	Antennæ.
	3. Premandibular, or Intercalary (Tritocerebral).	Wanting in postembryonic life, except in Campodea.	Premandibular appendages (in Campodea).
	4. Mandibular.	Epicranium behind the antennæ, genæ.	Mandibles.
	5. First Maxillary.	Epicranium, hinder edge? tentorium.	First maxillæ.
	6. Second Maxillary, or labial.	Occiput.	Second maxillæ, or labium. Postgula, gula, submentum, mentum, hypopharynx (lingua, ligula), paraglossæ, spinneret.

Upon anatomical grounds, different observers have recognized from one to seven head segments. As mentioned by Packard ('**98**, p. 50), Burmeister found but two; Carus and Audouin three; MacLeay, Newman, and Newport four; Straus-Durckheim seven. Huxley ('**78**, p. 343) said: "It is hardly open to doubt that the mandibles, the maxillæ, and the labium answer to the mandibles and the two pairs of maxillæ of the crustacean mouth. In this case, one pair of antennary organs found in the latter is wanting in insects, as in other air-breathing Arthropods, and the existence of the corresponding somite cannot be proved. But if it be supposed to be present, though without any appendage, and if the eyes be taken to represent the appendages of another somite, the insect-head will contain six somites." . . .

Huxley's conclusions were the most satisfactory that could be derived from a study of the completed organs alone, and reduced the problem to these questions: Do the eyes represent a somite? Is another antennal segment represented in insects? Do the labrum and hypopharynx represent distinct segments?

Authors began to realize the impossibility of settling the problem upon purely anatomical data, and attacked it from the embryological side.

Packard ('**71**, p. 21) concluded, "Accordingly, we seem forced to the belief that the head of the hexapodous insects consists of but *four* segments, *i. e.* the second maxillary, first maxillary, and mandibular segments, situated behind the mouth opening, and the antennary, or first and pre-oral segment, situated in front of the mouth. . . . The clypeus and labrum are apparently differentiated from the cephalic lobes, and thus seem to form a portion, or fold, of the antennary segment." Graber ('**79**) reached the same conclusion.

Viallanes, after carefully studying the development of the nervous system in Insects and decapod Crustacea, wrote the most important contribution upon the subject that has yet been published, and gave his results as follows ('**87**, pp. 108–109): —

"1. Le cerveau des Insectes, comme le cerveau des Crustacés décapodes, est formé de trois segments : j'appelle le premier *protocérebron* (cerveau du premier zoonite) ; le deuxième, *deutocérébron* (cerveau du deuzième zoonite) ; le troisième, *tritocérébron* (cerveau du troisième zoonite).

"2. Nous retrouvons, dans le protocérébron de l'Insecte, toutes les parties constitutives du protocérébron du Crustacé. Dans cette première région cérébrale, la seule différence qui s'observe entre les deux types est la suivante : chez l'Insecte les deux lobes protocérébraux viennent se souder sur la ligne médiane et se mettre ainsi en contact avec le protocérébron moyen. Chez le Crustacé, au contraire, les lobes protocérébraux sont très écartés de la ligne médiane et logés dans les pédoncules oculifères. Le rapprochement qui, chez l'Insecte, s'effectue entre les lobes protocérébraux, entraîne la disparition, ou pour mieux dire le raccourcissement extrême du tractus nerveux connu chez les Crustacés sous le nom de nerf optique.

"3. La deutocérébron, qui a une structure extrêmement caractéristique, se retrouve chez l'Insecte et chez le Crustacé avec les mêmes caractères et les mêmes connexions. Il en résulte que le nerf *antennaire* de l'Insecte est l'homologue du nerf de *l'antennule* du Crustacé.

"4. Chez le Crustacé le tritocérébron se compose des deux lobes antennaires et des deux ganglions œsophagiens (improprement appelés mandibulaires) et d'une commissure *sous*-œsophagienne (la commissure transverse de l'anneau œsophagien) qui réunit ces derniers. Le lobe antennaire donne naissance au nerf de l'antenne externe, le ganglion œsophagien à la racine du premier ganglion viscéral impair (ganglion stomatogastrique) et au nerf du labre.

"Chez l'Insecte, le tritocérébron subit une importante réduction, les lobes et les nerfs antennaires disparaissent, mais les représentants des ganglions œsophagiens (que j'ai décrits sous le nom des lobes tritocérébraux) subsistent dans leur intégrité. Comme chez le Crustacé, ils donnent naissance à la racine du premier ganglion viscéral impair (ganglion frontal) et au nerf du labre; comme chez les Crustacés, ils sont unis l'un à l'autre par une commissure *sous-œsophagienne* (commissure transverse de l'anneau œsophagien). Ainsi:

"Le nerf de l'antenne externe du Crustacé n'est pas représenté chez l'Insecte.

"Le nerf du *labre* de l'Insecte est l'homologue du nerf du *labre* du Crustacé."

After a lengthy discussion of the segmentation of the head, Viallanes concludes ('87, pp. 117–118): —

"1. La tête de l'Insecte est formée par six zoonites, trois sont pré-buccaux et trois post-buccaux.

"2. Le premier zoonite porte les yeux composés et les ocelles. Le deuxième les antennes. Le troisième, *qui est dépourvu d'appendices*, porte le labre, pièce qui, pas plus chez les Insectes que chez les Crustacés, ne peut être considérée comme le résultat de la soudure de deux appendices.

"3. Le quatrième zoonite porte les mandibules, le cinquième les mâchoires, le sixième la lèvre inférieure."

Wheeler ('93), Heymons ('95^{a}), and others have confirmed these conclusions.

Heymons ('95^{a}, p. 36), in a valuable paper on the segmentation of the insect-body, says, "Der Kopf besteht aus sechs Körperabschnitten: dem Oralstück, Antennensegment, Vorkiefersegment, und drei Kiefersegmenten."

Rudimentary intercalary appendages have been found in Anurida (Wheeler, '93) and Campodea (Uzel, '97^{b}). Claypole ('98) and Uzel ('98) have homologized them with the second antennæ of Crustacea.

Six somites are the most that have been admitted upon embryological grounds, but I am convinced that there are more than six.

Hansen ('93) suggested that the so-called "paraglossæ" [superlinguæ] of Machilis were homologous with the Crustacean first maxillæ, and my observations upon the development of the superlinguæ support his view. The superlinguæ originate independently as a pair of simple papillæ — like the mandibles and maxillæ — intermediate between the mandibles and the "first maxillæ," and represent a distinct, though reduced, segment, because provided with a ganglion. More conclusive proof could hardly be expected.

The insect-head, then, is composed of seven somites, which are homologous with the first seven of decapod Crustacea.

If the conclusions I have drawn in this paper are valid, certain radical changes become necessary in the commonly accepted ideas of homology among the great classes of Arthropods. These changes I submit in the following table : —

TABLE OF EQUIVALENT SOMITES IN THE HEAD OF ARTHROPODA.

Segment	*Arachnida*	*Chilopoda*	*Diplopoda*	*Crustacea*	*Hexapoda*
1	......	....	....	Compound eyes and ocelli	Compound eyes and ocelli
2	......	Embryonic præantennæ.	....	First antennæ	Antennæ
3	......	Antennæ	Antennæ	Second antennæ	Intercalary appendages
4	Chelicerræ	Mandibles	Mandibles	Mandibles	Mandibles
5	Pedipalpi	First maxillæ	Gnathochilarium	First maxillæ	Superlinguæ
6	First legs	Second maxillæ		Second maxillæ	Maxillæ
7	Second legs	Maxillipedes	....	First maxillipedes	Labium

Summary.

The protocerebrum of Apterygota agrees with that of other insects in development and structure. The ocular segments of Hexapoda and decapod Crustacea, as well as the compound eyes of the two groups, are homologous.

The labrum and clypeus of insects develop from a single median evagination between the procephalic lobes, and do not represent a pair of appendages. The labrum of Apterygota is homologous with that of other insects, as well as that of Symphyla, Diplopoda, Chilopoda, and the higher Crustacea.

The antennæ of Apterygota evaginate from the posterior boundaries of the procephalic lobes, and therefore agree with those of Pterygota in this respect. In both groups the antennæ are at first post-oral and subsequently pre-oral in position.

The deutocerebrum of insects is homologous with that of Crustacea, and the antennæ of Hexapoda are equivalent to the antennules of Crustacea and the embryonic præantennæ of Chilopoda.

Premandibular, or intercalary, appendages exist in the embryo of Anurida, and appear to be represented even in the adults of several Apterygote genera. The tritocerebrum of Apterygota is homologous with that of Orthoptera and decapod Crustacea, and the rudimentary premandibular appendages of Collembola and Thysanura represent the second antennæ of decapod Crustacea and probably the antennæ of Diplopoda and Chilopoda. A distinct primitive ganglion occurs in the intercalary segment of Anurida, therefore the segment must be regarded as one of the primary head-segments.

The mandibles of Apterygota develop from a pair of simple papillæ, the bases of which become oblique. No trace of lobation occurs except in Campodea. The mandibles of Collembola and Thysanura are homodynamous with the maxillæ and homologous with the mandibles of Pterygota, Scolopendrella, Crustacea, and probably Diplopoda and Chilopoda.

The "hypopharynx" in Apterygota is a compound structure consisting of two dorsal "superlinguæ," — as I have called them, — which develop from a pair of papillæ between the mandibular and first maxillary segments, and also a ventral lingua, which originates independently as a median unpaired evagination on the first maxillary segment. The two chitinous "lingual stalks," which are most highly developed among Apterygota, arise in superficial grooves of the ectoderm. The hypopharynx of Apterygota is undoubtedly homologous with that of Pterygota; although, in the latter group, the lingua and superlinguæ become united together and the lingual stalks become rudimentary. In Anurida a distinct neuromere exists for the "superlinguæ;" therefore it is necessary to recognize the superlingual segment as equivalent in morphological value to the other primary somites. The superlinguæ are homologous with the first maxillæ of Malacostraca and Chilopoda and are anatomically represented in the labial plate of Diplopoda. In order to avoid confusion, the terms "paraglossæ" and "ligula" should not be applied to the constituents of the hypopharynx, but are better restricted to the labium of insects. The lingua of Hexapoda is equivalent to the Crustacean hypopharynx, and possibly also to the median component of the Diplopod gnathochilarium.

The first maxillæ in Collembola and Thysanura develop essentially as in Orthoptera and may be homologized part for part with the maxillæ of generalized Pterygota. In Anurida a palpus appears in the embryo, but is resorbed before hatching, indicating the derivation of this genus from a form in which the first maxillary palpi were functional, as they are at present in Orchesella, Tomocerus, and other Collembolan genera. The first maxillæ of Campodea are clearly to be homologized with the first of Scolopendrella, the second of Chilopoda, and less clearly with the lateral portions of the Diplopod gnathochilarium. The first maxillæ of insects pass through a biramous condition, as in Crustacea, and the sclerites of these organs appear to be homologous in the two groups; the first maxillæ of Hexapoda, however, are equivalent to the second maxillæ of Malacostraca.

The labium in Anurida develops from a pair of papillæ, from which the entire gular region is derived. A palpus appears, but is soon resorbed, and no galeal and lacinial lobes are differentiated. Upon the whole, the labium among Apterygota is homologous with the same structure of Pterygota, although fewer sclerites are formed in the former group. The labium in insects, homodynamous with the mandibles and first maxillæ, agrees in detail with the first maxillipedes of decapod Crustacea. The labium of Campodea is homologous with the "second maxillæ" of Scolopendrella and the maxillipeds of Chilopoda, and is represented in the gnathochilarium of Diplopoda.

The sides of the face in Anurida develop from two lateral evaginations of the germ band near the mandibular segment, which eventually involve the labral and labial fundaments and complete the buccal cone. The mouth-folds of Collembola, Campodea, and Japyx are strictly homologous with the genæ of Pterygota. The dorsal region of the skull in Anurida does not differentiate into sclerites which may be compared with those of Pterygote insects.

The tentorium is inferred to develop from cells which have been proliferated from the ectoderm.

The evidence convinces me that there are just seven somites in the head of Anurida, and that probably the same is true for all Hexapoda. The cephalic somites are successively: ocular, antennal, intercalary, mandibular, superlingual, maxillary, and labial. As I have found embryonic ganglia for the intercalary and superlingual segments, there are seven cephalic ganglia, one for each somite. Moreover, excepting the ocular segment, every somite is represented by a pair of appendages. I find no evidence whatever for more than seven primitive cephalic segments, and believe that my observations have assisted to settle the long-disputed question of the segmentation of the head.

Since the time of Fabricius, the mouth-parts of insects have been of primary importance for the systematist. While insisting that a logical classification must recognize *all* anatomical structures, it must be admitted that the mouth-parts are of fundamental systematic value on account of the range of their differentiation.

Without discussing at length the phylogeny of insects, I may briefly give the bearing of these studies upon the subject, remarking that my conclusions are in entire accord with approved views upon the origin of insects.

The Collembola are strikingly like Campodea and Japyx in structure, their peculiar entognathous characteristic separating these three groups from all other insects. The Collembola as a group are somewhat more specialized than the Thysanura in general structure. The Smynthuridæ, with their globular bodies, vertical heads, and well-developed furculæ and ventral tubes, represent one extreme of differentiation — comparatively high. The Aphoruridæ, including Anurida, with vermiform bodies, subequal segments, horizontal heads, no furcula, etc., are much more generalized, and probably degenerate forms. Anurida, for example, has both pairs of maxillary palpi, as well as rudimentary abdominal appendages and the fundaments of a furcula in the embryo, but in the embryo only. Therefore the ancestral Collembolan was probably intermediate between Smynthuridæ and Aphoruridæ, and is most nearly represented by members of the family Poduridæ. The resemblance in the mouth-parts leads us to suppose that the primitive Collembolan descended from the stem form of Campodea and not far below Campodea itself.

The affinities of Campodea, which is slightly more primitive than Japyx, are in two directions: towards Machilis and Lepisma on the one hand, and towards Scolopendrella on the other. In the first two genera the mouth-parts are clearly derivable from the Campodean type, and link Campodea with Orthoptera. In regard to Scolopendrella, it was long uncertain whether it should be placed among Thysanura or Myriopoda, on account of its strong affinities for both. Most authors have followed Grassi and placed it in the latter group, always admitting its insectean features. In the mouth-parts, Scolopendrella approaches

Campodea rather than Diplopoda, but is unquestionably nearer Diplopoda than it is to Chilopoda.

The gnathochilarium of Diplopoda may be homologized with the appendages of three hexapod somites, but only two embryonic segments have as yet been found; and the subject needs further investigation.

The mouth-parts of Chilopoda may be homologized with those of insects in only the broadest way, the correspondences being principally those of position.

Between decapod Crustacea and Apterygota there are decided morphological resemblances. The seven cephalic somites which I have found in the latter group I have homologized in detail with the anterior seven of the former, and pointed out that most of the homologous appendages function alike in the two groups. These homologies, however, simply indicate a partial parallelism in development; for in most respects Crustacea and Hexapoda are very divergent classes.

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Извѣстія Импèр. Общест. Любит. Естест., Антропол. и Этногр. Томъ xliii. Вып. 1.
[Contributions to the Knowledge of the Embryological Development of Geophilus ferrugineus L. K. and Geophilus proximus L., K. Studies Lab. Zool. Mus. Moscow Univ., Vol. 2, Pt. 1. 77 pp., 108 fig.]

EXPLANATION OF PLATES.

All figures were drawn with the aid of a camera lucida, from preparations of Anurida maritima Guèr.

ABBREVIATIONS.

add.	Adductor.
app. ab.$^{1-3}$	Abdominal appendages, 1st, 2d, 3d.
app. pr'md.	Premandibular appendages.
app. thx.$^{1-3}$.	Thoracic appendages, 1st, 2d, 3d.
at.	Antenna.
atc.	Articulation, or hinge.
ba., ba'.	Base.
br. d.	Dorsal arm.
br. p.	Posterior arm.
cav. buc.	Buccal cavity.
cd. v.	Ventral cord.
cdx.	Pivot.
cht.	Chitin.
clyp.	Clypeus.
coel.	Coelom (body cavity).
cpt.	Head.
c'stt.	Constrictor.
cta.	Cuticula.
d.	Dorsal.
de.	Teeth.
dep.	Depressor.
deu'ceb.	Deutocerebrum.
dil.	Dilator.
dt.	Duct.
ec'drm.	Ectoderm.
ga.	Galea.
gn. inf'œ.	Infra-œsophageal ganglion.
gn. su'œ.	Supra-œsophageal ganglion.
h'drm.	Hypodermis.
i.	Intima.
i'cis.	Incisive.
lab.	Labium.
lbr.	Labrum.
lcn.	Lacinia.
lng.	Lingua.
ln. v.	Linea ventralis.
lvt.	Elevator.
mb.	Membrane.
mb. rug.	Corrugated membrane.
md.	Mandible.
ms'drm.	Mesoderm.
mu.	Muscle.
mx.^{1}	First maxilla.
mx.^{2}	Second maxilla.
nl. gn.	Ganglionic nucleus.
ocl.	Ocellus.
o. d.	Dorsal organ.
œ.	Œsophagus.
o. p'at.	Post-antennal organ.
or.	Mouth.
pd.	Foot.
pd'.	Footstalk.
phy.	Pharynx.
pig.	Pigment.
pli.	Fold.
pli. or.	Mouth fold.
plp.	Palpus.
pr'ceb.	Protocerebrum.
prd.	Proctodeum.
prj.	Projection.
pr't. l.	Lateral protrusor.
pr't. ms.	Mesal protrusor.
ret.	Retractor.
sng. cp'.	Blood corpuscle.
sta.	Stirrup.
stmd.	Stomodeum.
stp.	Stipes.
sul.	Trough.
sul. n.	Neural groove.
su'lng.	Superlingua.
sut.	Suture.
sut. m.	Median suture.
tœ. g.	Germ band.
tnt.	Tentorium.
tri'ceb.	Tritocerebrum.
v.	Ventral.
yk.	Yolk.

PLATE 1.

Figs. 1–6 represent views of the left side of eggs (embryos) at Stages 1 to 6 respectively, with the outer egg membrane removed. × 150.

PLATE 2.

Fig. 7. View of left side of embryo at Stage 7, with the outer egg membrane removed. × 150.

Fig. 8. Ventral aspect of germ band at Stage 1. × 150.

Fig. 8a. Ventral aspect of a portion of the germ band at Stage 1 more highly magnified. × 480.

Fig. 9. Left aspect of cephalic region at Stage 3. × 480.

Fig. 10. Right aspect of cephalic region at Stage 3. × 480.

Figures 9 and 10 are from the same preparation.

DEVELOPMENT ANURIDA. PLATE 2.

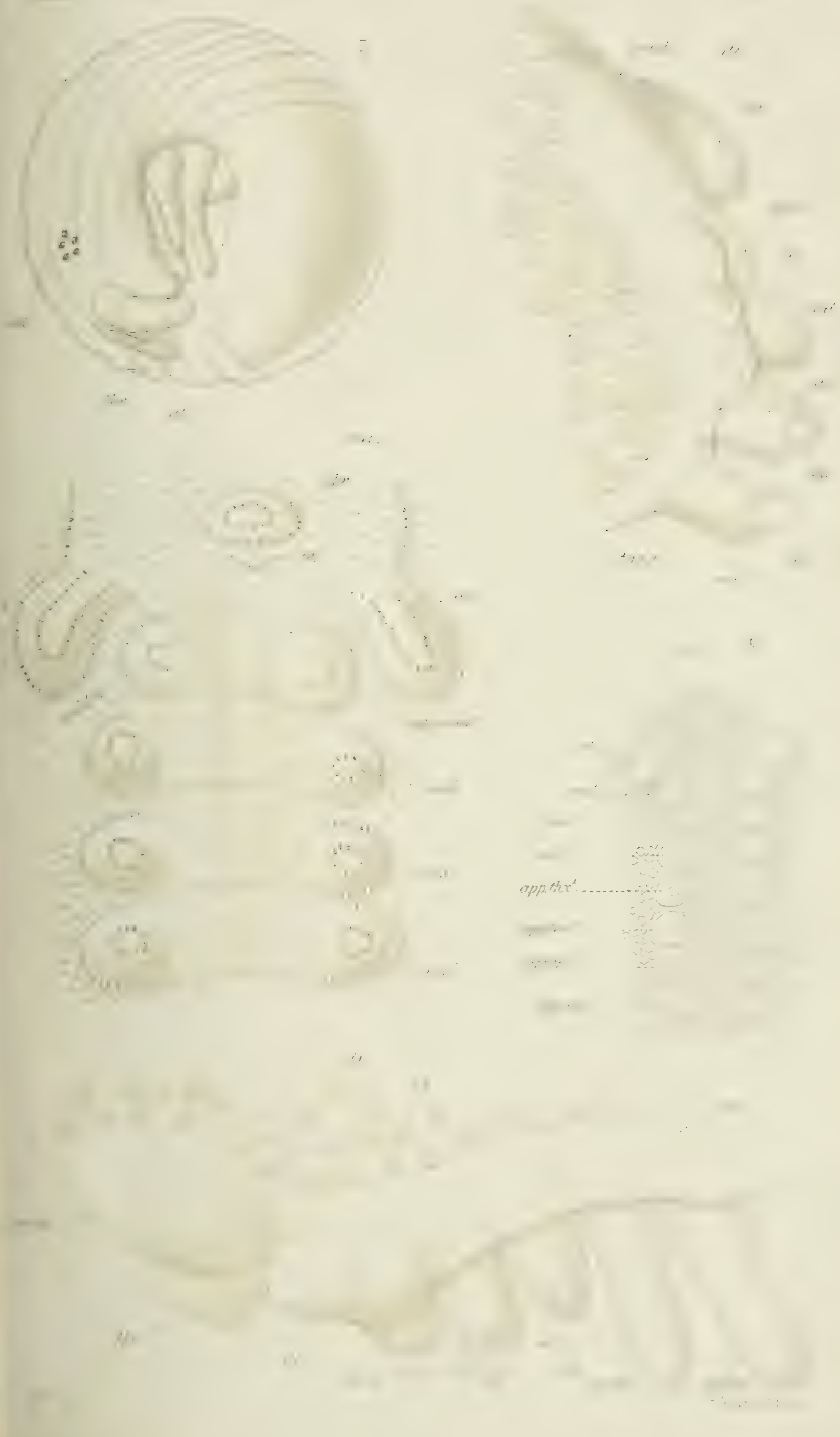

PLATE 3.

Fig. 11. Ventral aspect of cephalic region of germ band at Stage 3. × 480.
Fig. 12. Ventral aspect of cephalic region of germ band at Stage 4. × 480.
Fig. 13. Sagittal section of labrum at Stage 3. × 762.
Fig. 14. Transection of germ band at the labial segment in Stage 3. × 762.
Fig 15. Transection of germ band at the first maxillary segment in Stage 3. × 762.
Fig. 16. Transection of germ band at the mandibular segment in Stage 3. × 762.
Fig. 17. Posterior aspect of left first maxilla at Stage 3. × 480.
Fig. 18. Posterior aspect of left second maxilla at Stage 3. × 480.
Fig. 19. Left aspect of germ band at Stage 4. × 480.
Fig. 20. Left aspect of cephalic region at Stage 5. × 480.
Fig. 21. Ventral aspect of cephalic region at Stage 5. × 480.
Fig. 22. Posterior aspect of left first maxilla at Stage 5. × 480.

The last three figures are from the same preparation.

PLATE 4.

Fig. 23. Anterior aspect of a transection of germ band at mandibular segment in Stage 7. The section being thick shows both mandibles and, behind them, the superlinguæ. × 762.

Fig. 24. Left aspect of embryonic head, represented as if transparent, at Stage 7. × 480.

Fig. 25. Ventral aspect of lingua and first maxilla at Stage 7. × 480.

Fig. 26. Dorsal aspect of head of right maxilla at Stage 8. × 762.

Fig. 27. Dorsal aspect of lingua and superlinguæ at Stage 7. × 762.

Fig. 28. Paramedian section to show the primitive cephalic ganglia at Stage 5. × 762.

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PLATE 5.

Fig. 29. Ventral aspect of head, represented as if transparent, at Stage 7. × 480.

Fig. 30. Anterior aspect of mouth-parts at Stage 7. From the same preparation as Figures 24 and 29. × 480.

Fig. 31. Paramedian section of head at Stage 7. × 480.

Fig. 32. Ventral aspect of left maxilla at Stage 7. × 762.

Fig. 33. Dorsal aspect of adult head. × 45.

Fig. 34. Anterior aspect of mouth at Stage 8. × 480.

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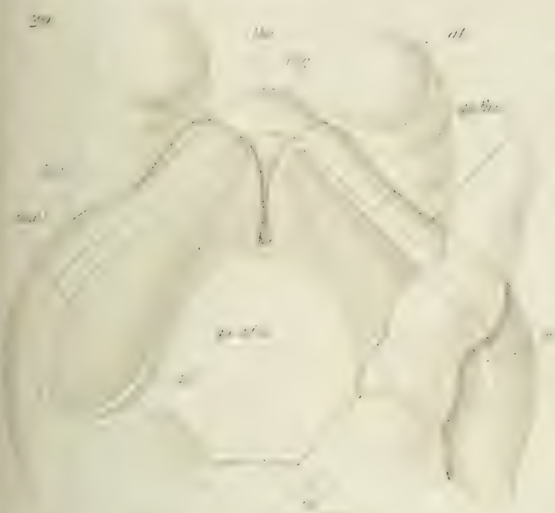

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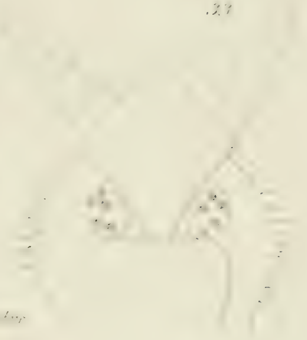

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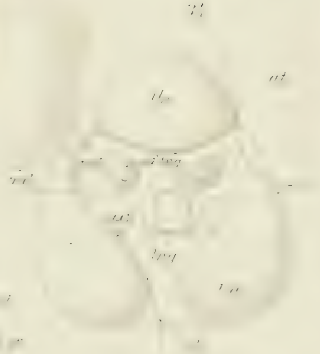

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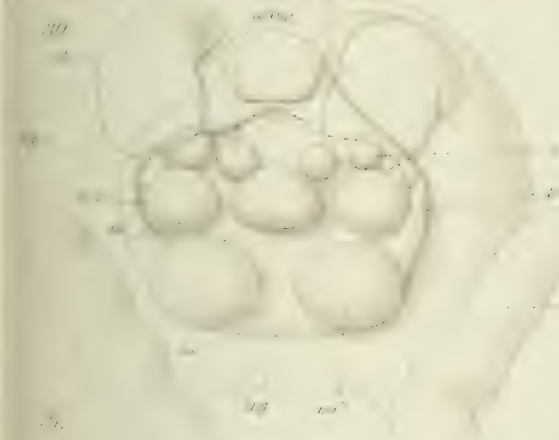

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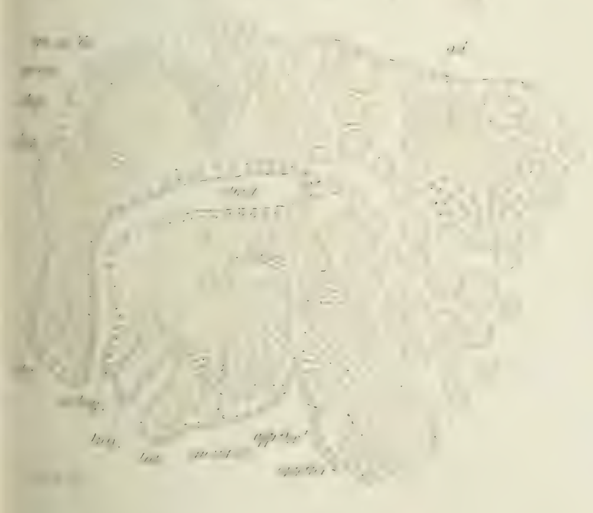

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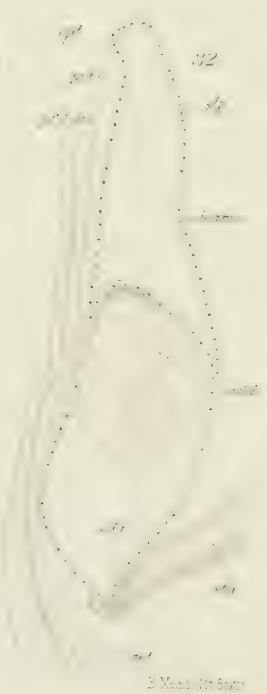
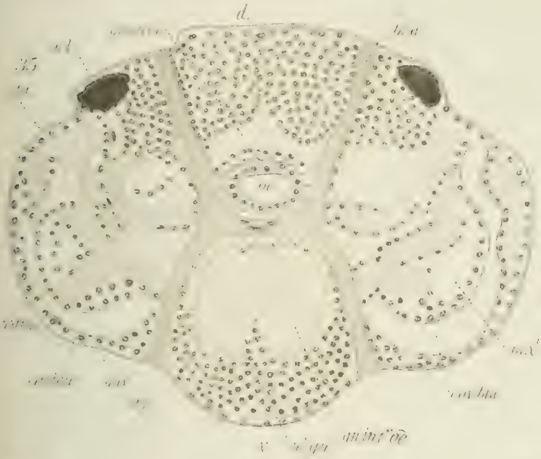


B Meisel lith Boston

PLATE 6.

Fig. 35. Transverse slightly oblique section of head at Stage 8. × 480.
Fig. 36. Dorsal aspect of left mandible of adult. × 150.
Fig. 37. Dorsal aspect of anterior extremity of adult right mandible. × 480.
Fig. 38. Dorsal aspect of skeletal structure of internal mouth-parts *in situ*. × 150.
Fig. 39. Dorsal aspect of head of left maxilla in adult. × 480.
Fig. 40. Surface view of finished labrum. × 150.
Fig. 41. Head of adult insect viewed from the left side. × 150.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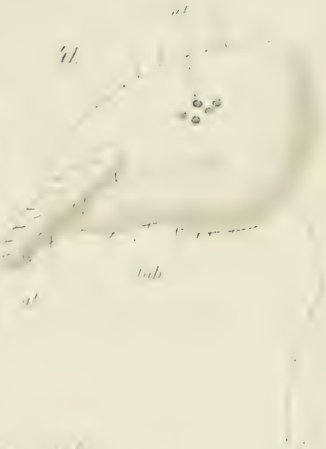
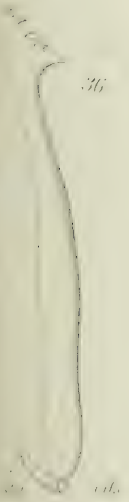
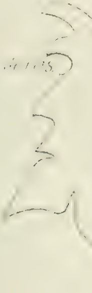
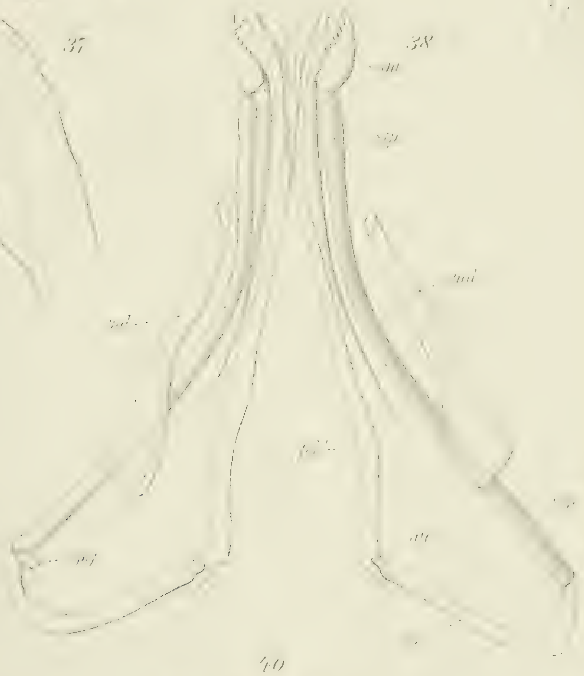
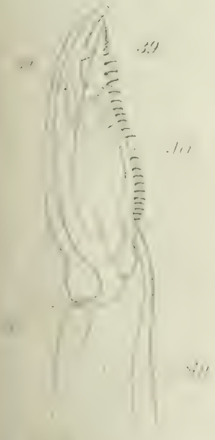
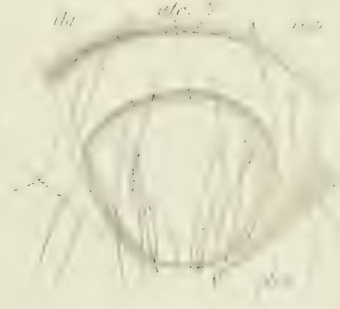












F. Meisel, lith. Boston.

PLATE 7.

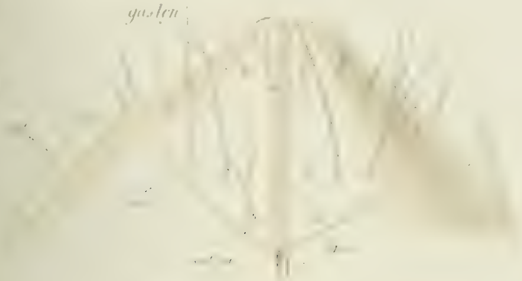
Fig. 42. Dorsal aspect of completed lingua and superlinguæ. × 480.

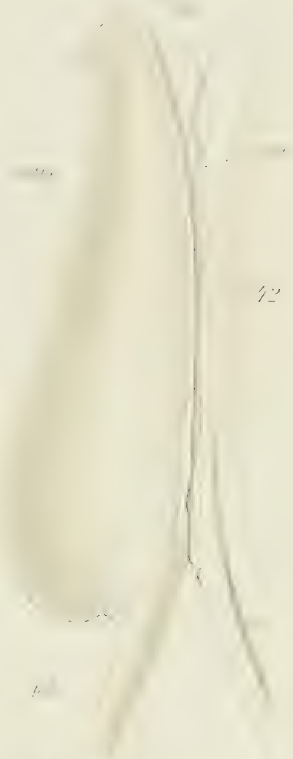
Fig. 43. Surface view (ventral) of adult labium. × 150.

Figs. 44–50. Transections of internal mouth-parts of adult to show their relations to each other and to the buccal cavity.

Fig. 44 is the most anterior of the series; Fig. 50 the most posterior.

Figs. 44 and 45 are magnified 350 diameters, Figs. 46–50, 480 diameters.





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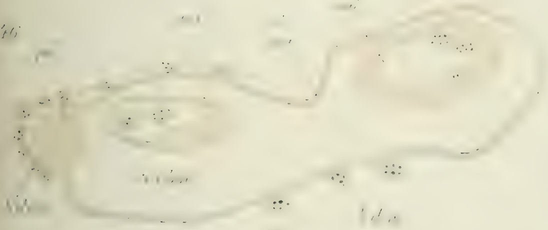

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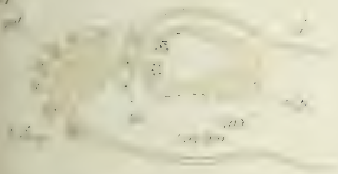
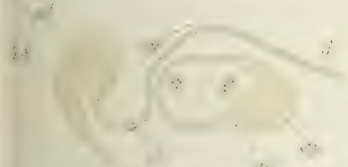
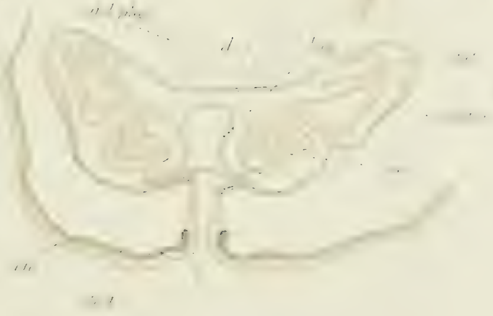
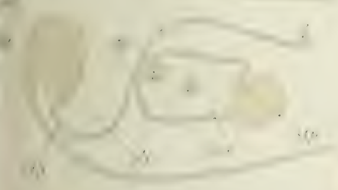
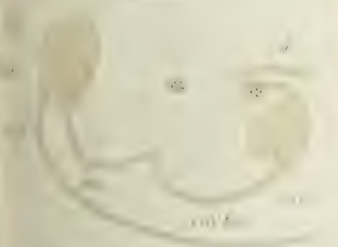










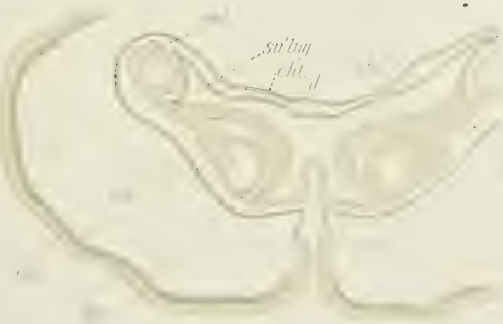
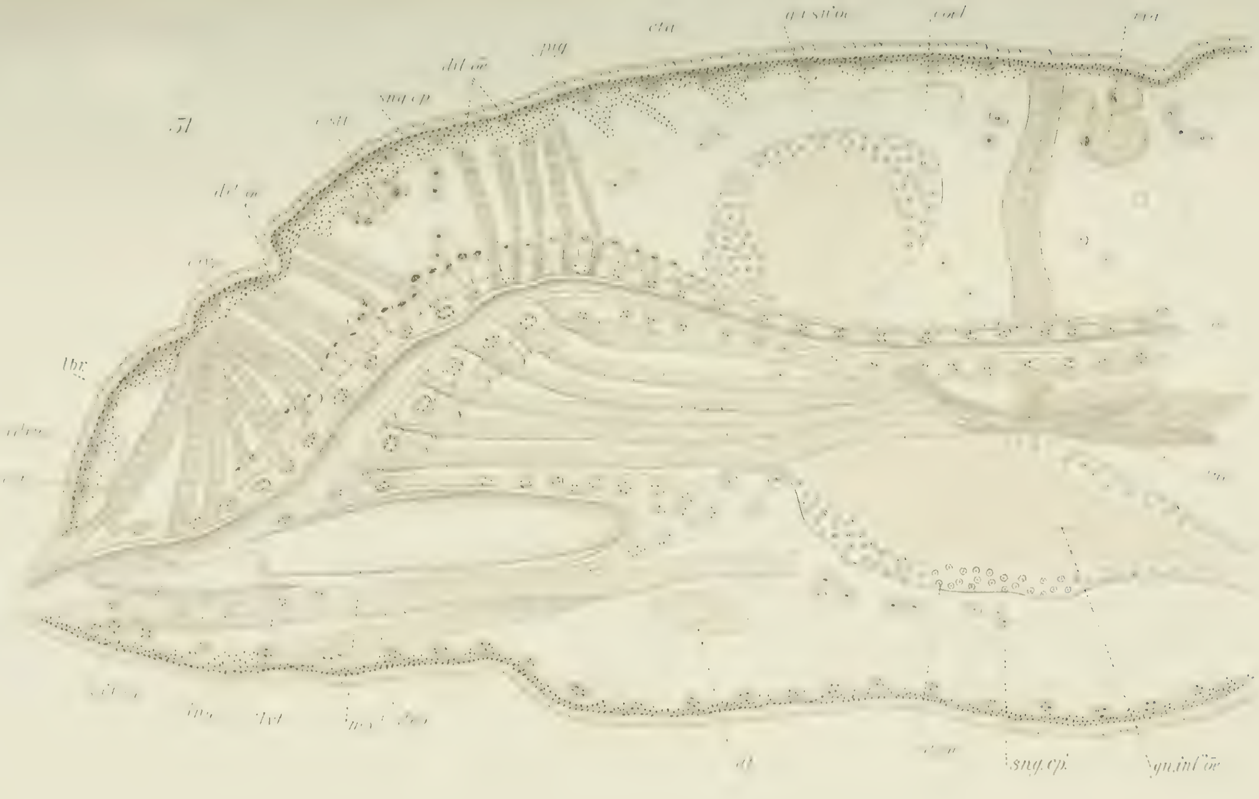


PLATE 8.

Fig. 51. Reconstruction of part of the left side of the adult head, from sections taken near the median plane. × 350.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Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
Vol. XXXVI. No. 6.

REPORTS ON THE DREDGING OPERATIONS OFF THE WEST COAST OF CENTRAL AMERICA TO THE GALAPAGOS, TO THE WEST COAST OF MEXICO, AND IN THE GULF OF CALIFORNIA, IN CHARGE OF ALEXANDER AGASSIZ, CARRIED ON BY THE U. S. FISH COMMISSION STEAMER "ALBATROSS," DURING 1891, LIEUT. COMMANDER Z. L. TANNER, U. S. N., COMMANDING.

XXVIII.

DESCRIPTION OF TWO NEW LIZARDS OF THE GENUS ANOLIS FROM COCOS AND MALPELO ISLANDS.

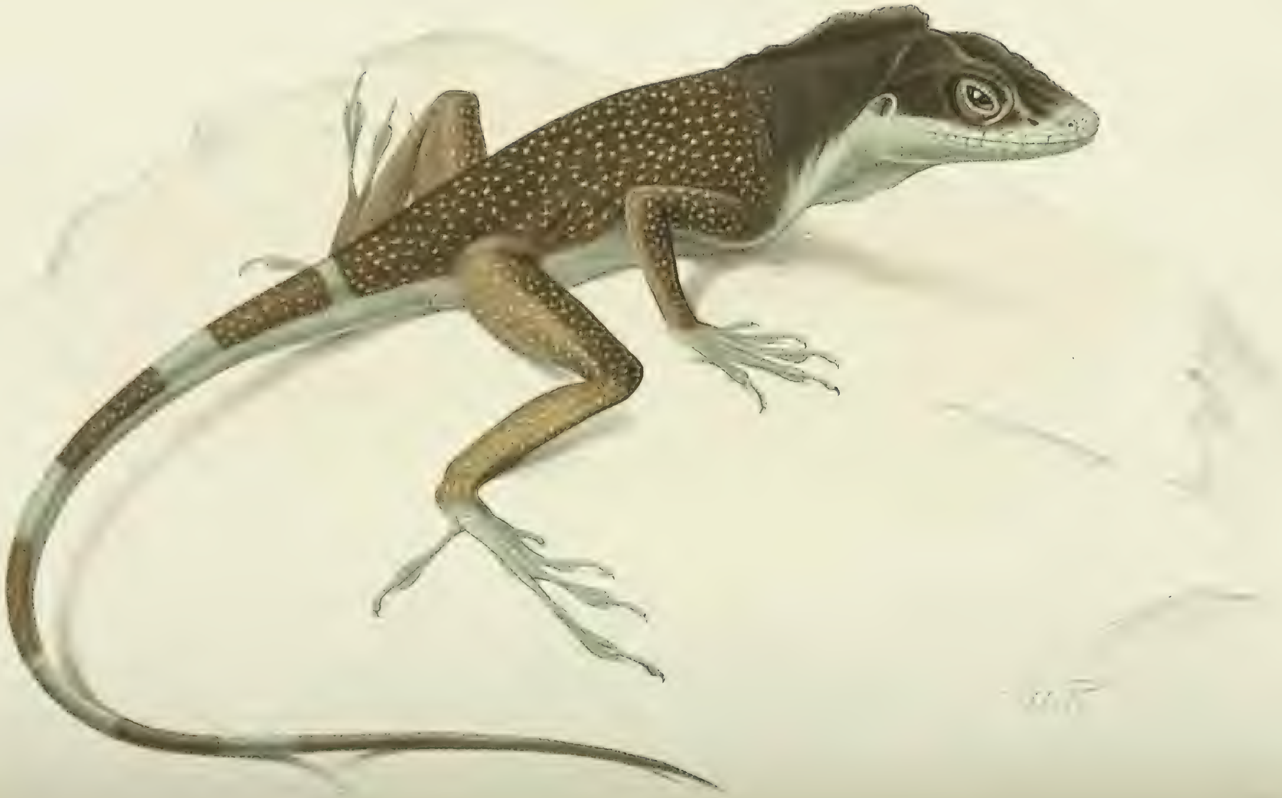
By Leonhard Stejneger.

[Published by Permission of Marshall McDonald and George M. Bowers, U. S. Fish Commissioners.]

With One Plate.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
November, 1900.

ANOLIS



No. 6. — *Report on the Dredging Operations off the West Coast of Central America to the Galapagos, to the West Coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish Commission Steamer "Albatross," during* 1891, LIEUT. COMMANDER Z. L. TANNER, U. S. N., *Commanding.*

XXVIII.

Description of two new Lizards of the genus Anolis from Cocos and Malpelo Islands. BY LEONHARD STEJNEGER.

The two Anoles here described were the only reptiles obtained on the islands of Cocos and Malpelo during the expedition. Each species is peculiar to the island upon which it is found. Of the two, the one from Malpelo seems to be most highly specialized, there being no nearly related species on the mainland with which I am familiar, while the species from Cocos Island belongs to a group which has a number of representatives in Central America. The two species are only distantly interrelated, inasmuch as they belong to widely separated sections of the genus.

It is quite possible that a more thorough search on Cocos Island might reveal additional reptiles. In fact, Mr. Townsend informs me that he saw a snake there which escaped.

Anolis agassizi,[1] sp. nov.

Diagnosis. — Tail cylindrical, without crest or keel; dorsal scales keeled, subequal to those on the flanks, slightly smaller than the ventrals, and separated from each other by one or more rows of minute granules; ventral scales keeled; digital expansions very large; about thirty-six transverse lamellæ under ii and iii phalanges of fourth toe; occipital scale about as large as ear-opening; scales of supraorbital semicircles very much enlarged (forming high, tuberculated crests in the adults), and separated by one row of small scales; occipital separated from supraorbital semicircles by one or two series of scales; supraocular scales rough or rugose, sometimes irregularly keeled; canthus rostralis sharp; mental shield single. with a deep sulcus posteriorly, very large; tibia nearly equalling the head in length, and at least as long as distance from mouth to ear-opening; scales on under side of tail twice as large as those on the upper side, all keeled; scales on dorsal surface of hands and feet multi-carinate. Adults with a high longitudinal cervico-nuchal flap; males with enlarged post-anal scales.

---

[1] Named in honor of Professor Alexander Agassiz.

Habitat. — Malpelo Island, Pacific Ocean, off Columbia, South America.

Type. — U. S. National Museum, No 22101; March 5, 1891; collector, Chas. H. Townsend.

Description. — ♂ ad. U. S. Nat. Mus. No. 22101. Head once and two thirds as long as broad, slightly longer than tibia; frontal and occipital regions deeply concave; supraorbital ridges high, bony, surrounding the occipital hollow, and nearly joining behind it at the beginning of the cervico-nuchal fold; anteriorly they divide and continue mesially as frontal ridges which converge on the snout, meeting some distance behind the level of the nostrils, while externally they join the supraciliary ridge, and in company the latter extend to under the nostrils as a strong canthus rostralis, thus forming a deep valley on each side between the canthus and the frontal ridge; there is also a post-superciliary ridge extending to above the ear-opening, and with a valley between it and the occipital ridge; scales of supraorbital semicircles very much enlarged, forming high tuberculated bony crests, separated by a single series of very small scales; scales forming frontal ridges and valleys rather large, irregularly hexagonal, concave or convex according to situation; scales on snout smaller, more irregular, elongate, four in contact with rostral; about seven larger supraocular scales, keeled or tuberculated, separated by one row of granules from semicirculars; superciliary edge with two very elongated scales anteriorly, granular posteriorly; occipital scale slightly larger than ear-opening, separated from supraorbital semicircle by one row of scales; three canthal scales; loreal region with two deep hollows, the posterior one largest; loreal rows four; a series of large suboculars, of which the one below the posterior angle of the eye descends to the edge of the lip; rostral very wide and very low, four times as wide as high, nearly rectangular; six to seven low supralabials in front of the subocular edging the lip, decreasing in height posteriorly; ear-opening rather small, oval, vertically oblique; nape and neck with a high, flexible dermal crest or flap on the middle line, almost co-extensive with the poorly developed dewlap underneath; several dermal folds and wrinkles on sides of neck; mental shield large, with a deep sulcus behind; gular scales small, feebly keeled; body feebly compressed; dorsal scales slightly larger than those on flanks, a few series along the median line decidedly, though not abruptly larger, all more or less distinctly keeled and surrounded by one or more minute granules; ventral scales slightly larger than dorsals, rhomboidal, imbricate, keeled, about five to six in the distance between nostrils; scales on anterior surfaces of limbs larger than ventrals, keeled, those on dorsal surface of hands and feet multi-carinate; adpressed hind limb reaches halfway between eye and nostral; digital expansions very large, thirty-six transverse lamellæ under ii and iii phalanges of fourth toe; tail less than twice the length of head and body, cylindrical, without crest or keel; scales on tail larger than ventrals, straight, in transverse rows, but with scarcely an indication of verticels, those on the lower surface nearly twice as large as those above; a pair of enlarged post-anal scales. Color of live specimen (according to the sketch of Mr. Magnus Westergren, the artist of the expedition): top and sides of head and neck uniform sooty black gradually merging into the ground color of the upper surface of body, which is "Vandyke" brown, sprinkled with minute dots of an ochraceous buff; upper surface of limbs as well as alternate cross-bands on tail similarly colored; the hands and feet as well as the intervals between the crossbands pale "Nile" blue; end of snout, lips, and entire under side similarly bluish white. In alcohol the ground color is more blackish and the dots less yellowish.

DIMENSIONS.

Total length	271 mm.
Snout to ear-opening	26 "
Snout to vent	101 "
Tail from vent	170 "
Fore limb	50 "
Hind limb	90 "
Tibia	26 "

Variation. — A large full-grown female (No. 22103) differs from the male described above only in the absence of enlarged post-anal scales. Two somewhat younger specimens (female, No. 22104, male, No. 22105) differ from the fully adult specimens chiefly in the lesser elevation of the cephalic crests and the total absence of the cervico-nuchal flap; the color of the back, which seems to be identical with that of the adults, extends also over the upper surface of neck and head.

Remarks. — Mr. Charles H. Townsend, who collected these specimens in Malpelo, informs me that they were running over the rocks near the water. The island was too steep to afford a landing, but the lizards were shot off or whisked off the face of the cliffs, thus falling into the water, whence they were secured by the collector.

Anolis townsendi,[1] sp. nov.

Diagnosis. — Tail subcylindrical; dorsal scales but indistinctly larger than those on the flanks, those on the vertebral region keeled; gular and ventral scales keeled; digital expansion strongly developed; occipital scale larger than ear-opening, separated from supraorbital semicircles by two or three scales, the semicircles separated by a similar number of scales; scales on upper surface of snout as well as enlarged supraoculars keeled; anterior half of superciliary ridge with three very long and narrow, strongly keeled scales placed obliquely; no markedly enlarged series of scales below infralabials; tibia measuring more than two thirds the length of head, slightly shorter than distance between end of snout and ear-opening; the adpressed hind limb reaches beyond the eye; tail more than once and a half as long as head and body.

[1] Named in honor of Mr. Charles H. Townsend.

Habitat. — Cocos Island, Pacific Ocean, off Costa Rica, Central America.

Type. — U. S. National Museum, No. 22106; Feb. 28, 1891; collector, Charles H. Townsend.

Description. — ♂ ad. U. S. Nat. Mus. No. 22106. Head twice as long as broad, longer than tibia; forehead slightly concave; frontal ridges nearly obsolete; upper head scales small, keeled; scales of supraorbital semicircles moderately enlarged, separated by three scales; enlarged supraorbitals numerous, elongated, sharply keeled, in contact with semicirculars; occipital shield elongate oblong, somewhat larger than ear-opening, separated from semicirculars by two scales; canthus rostralis very distinct, of six scales, the anterior ones small, the posterior two very long and narrow continued backwards in line with three superciliaries, which are also unusually long, narrow, and keeled; posterior half of superciliary ridge granular; a series of enlarged suboculars, keeled, not reaching lip; loreal rows, about six, keeled; eight supralabials to below centre of eye, rugose; ear-opening moderate, vertically oval; dewlap moderate with a thickened edge of densely set short thick scales, those on sides of appendage distant and very elongate; gular scales small, long, and narrow; dorsal scales much smaller than ventrals, and indistinctly larger than those on the flanks, and gradually but slightly increasing in size toward the vertebral line, where a few rows are distinctly keeled; no dorsal or cervical fold or crest; ventral scales larger, imbricate, keeled, like all the scales of the underside; scales on anterior surfaces of limbs somewhat larger than ventrals, keeled; tail subcylindric, scales about the size of ventrals, keeled, with hardly an indication of verticels; body compressed; adpressed hind limb reaches beyond eye; no enlarged post-anal scales. Color above dull brownish gray, irregularly and indistinctly mottled with dusky which shows a tendency to form cross-bars on the tail; limbs more brownish with lighter roundish spots; lores, temples, and sides of neck anteriorly with irregular white markings; a very distinct white, black-edged lateral band from sides of neck over the shoulder to groin; underside whitish; throat with indistinct, brownish mottlings.

DIMENSIONS.

Total length	123 mm.
Snout to ear-opening	13 "
Snout to vent	47 "
Tail from vent	76 "
Fore limb	22 "
Hind limb	37 "
Tibia	12 "

Variation. — A slightly smaller female (U. S. Nat. Mus. No. 22107) differs chiefly in the absence of a dewlap and in coloration; the white lateral band is present, but it is not edged with blackish, and there is in addition a narrow white vertebral band from occiput to root of tail.

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THE OTOCYST OF DECAPOD CRUSTACEA: ITS STRUCTURE, DEVELOPMENT, AND FUNCTIONS.

By C. W. Prentiss.

With Ten Plates.

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THE OTOCYST OF DECAPOD CRUSTACEA: ITS STRUCTURE, DEVELOPMENT, AND FUNCTIONS. By C. W. Prentiss.

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INTRODUCTION.

Since the appearance of the admirable paper by Hensen ('63) on the auditory organs of decapods, a period of thirty-seven years has elapsed, a period rich in zoölogical discoveries and improvement in general technique. The great advances made in comparative neurology by means of modern methods have reopened to investigators fields for research hitherto considered exhausted. The zoölogist of the present time is thus enabled to reap a second crop on ground already carefully gleaned, and to harvest results as important as those originally obtained.

The physiological work of Hensen's paper has been continued in recent years by various investigators. But aside from the paper by Bethe ('95) on the otocysts[1] of the schizopod Mysis, little work has been done on the morphology of the decapod ear since 1863.

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[1] Throughout this paper the terms otocyst, statocyst, ear, and auditory sac will be used synonymously to designate the auditory organ, so-called, of Crustacea.

To throw more light on our knowledge of the vertebrate ear, comparative study of the (perhaps) analogous organ found among invertebrates may be of great practical value. For by such comparative study zoölogists have been enabled to solve many perplexing questions which might otherwise have proved too difficult for solution.

The present study was undertaken with this practical bearing of the subject in mind, and with the hope that by the aid of modern neurological technique it would be possible to go deeper into many undecided questions than Hensen could.

The work is necessarily twofold in its scope, owing to the inseparable nature of the morphology and physiology of the auditory organ. We have, first, to obtain more accurate knowledge concerning the structure, innervation, and development of the decapod otocyst. In doing this especial attention must be given to the innervation, which must be compared with that of other sense organs in decapods. And, secondly, we must determine from evidence obtained by others in the past, and from additional physiological experiment, whether we are justified in ascribing a true auditory function to this much discussed apparatus.

PART I. — MORPHOLOGY.

A. HISTORICAL SURVEY.

Although the literature up to Hensen's time is well summarized by him, yet it may be worth the while to take a glance at what has been done, touching upon only the more important works, however, as a fairly complete list of authors is appended in the Bibliography.

The earliest notice of an ear in Crustacea is that of Minasi, a Dominican monk, who in 1775 attributed the sense of hearing to Pagurus, the hermit crab, and described as the auditory apparatus what is now known as the green gland or excretory organ of decapods. The organ supposed to subserve the function of hearing was thus from the very first misplaced, and its identity was in doubt even up to the time of Häckel (**'57**) and Leydig (**'57**), who were the first to rectify the erroneous ideas which existed in regard to the functions of the green gland and the otocyst.

The true sacs were, however, discovered and described as early as 1811 by Rosenthal (**'11**). He mentions the cavity, its opening, and nerve; but it was left for Treviranus (**'02–'22**, Bd. 6, pp. 308–310) to discover the sand, or otoliths, present in the otic chamber.

The first good description of the organ, accompanied by figures, was given by the Englishman Farre ('**43**), who carefully dissected the otocysts of the crayfish (Astacus fluviatalis), the European lobster (Astacus marinus), the hermit crab (Pagurus), and the rock lobster (Palinurus quadricornis).

The organs were found by Farre to be situated in the basal segment of the inner antennæ (antennules), the thin dorsal membrane of which in A. marinus he compared to the fenestra ovalis of the vertebrate ear. The openings of the sacs were always found to be large enough to admit the otoliths, which rest upon auditory bristles. The otoliths were, he maintained, merely grains of sand. The auditory bristles were briefly described, and their semi-circular arrangement noted; a nerve was traced from the brain to the ventral surface of the otocyst, where it formed a plexus. In Farre's opinion separate fibres probably supplied the bases of the different hairs. While the otocysts of the lobster, crayfish, and hermit crab were of relatively large size, nearly filling the basal segment of the antennule, their openings were very small and well guarded by a "chevaux de frise" of bristles. In Palinurus the organ was apparently degenerate; the sac small, shallow, with very large opening, and the auditory hairs sparse and irregularly arranged. The otoliths were of large size and few in number. The whole apparatus was held by Farre to be a delicately modified tactile organ, and he doubted if a *true auditory function* could be ascribed to it.

During the next twenty-five years otocysts were discovered and examined in various decapods by Souleyet ('**43**), Von Siebold ('**44**, '**48**), Leuckart ('**53**, '**59**), Frey und Leuckart ('**47**), Huxley ('**51**), Leydig ('**55**, '**57**, '**60**), Bate ('**55**, '**58**), Hensen ('**63**), Sars ('**67**), and Lemoine ('**68**). Leuckart und Frey ('**47**) briefly described the sacs which they found in the endopod of the last abdominal appendages of Mysis, mentioning the otolith and auditory hairs.

Leuckart ('**53**) made a comparative study of the otocysts in many crustacean forms. He divided them into two groups: — Those having (1) closed sacs with one otolith, and (2) open sacs with many otoliths. Leuckart's general descriptions agree with those of Farre.

Kroyer ('**59**) devotes a few pages of his monograph on Sergestes to a comparative account of this organ in different Crustacea. He follows Leuckart's method of grouping. To the first type (closed sacs, and one otolith) belong such forms as Lucifer, Sergestes, Mysis, and Phyllosoma. In the second group (open sacs and many otoliths) are placed Homarus, Astacus, and Palinurus. In the opinion of Kroyer, Farre erred in considering the otoliths simply particles of sand; for sometimes the sacs are closed, and again the openings are often too small to admit the passage of the otoliths from the exterior. They must be, then, deposits of calcium carbonate secreted by the animals themselves.

Hensen's (**'63**) account of the otocyst is far more complete than any other, and a fairly extensive review of his paper is necessary for the sake of later comparisons. He worked mostly with freshly collected animals, although some twenty-four species were studied from alcoholic material. His principal methods were dissection and maceration, some few crude sections, however, being made. The paper is divided into an anatomical and a physiological part. The latter portion will be reviewed, along with other papers of a similar nature, in Part II of this paper.

The elementary parts of the typical auditory organ are described by Hensen (**'63**, p. 326) thus: "Der Gehörapparat der höheren Krebse besteht nun, kurz gesagt, darin, dass, von der Endganglie eines Nerven ein feiner Faden in ein Chitinhaar hineintritt, und an einen eigenthümlich gebildeten Theil der Haarwand sich festsetzt. Diese Haarwand ist so locker mit der Schalenhaut verbunden, dass sie bei entsprechenden Tönen recht bedeutende Schwingungen vollführen kann und vollführt. Das Haar selbst geht zuweilen noch in oder zwischen Steine hinein."

Crustacea he divides into four classes according to the condition of otocyst and otoliths: —

1. Sacs closed, with one otolith: example, Mysis.
2. Sacs closed, without an otolith: all Brachiura.
3. Sacs open, many otoliths: Astacus, Palæmon.
4. No sac nor otoliths, but free auditory hairs.

Otoliths. In confirmation of Farre it was found that the otoliths of decapods having open ear sacs were mainly composed of grains of sand. This was proved by chemical tests, and by keeping newly moulted animals (Palæmon) in filtered water to which uric acid crystals had been added. Examination of the otocysts some time after moulting showed the presence of these crystals in the sac. In larger forms, such as the lobster and crayfish, the sand particles are spread over the whole basal surface of the ear sac. In shrimps and prawns they are more closely aggregated. The single otolith found in Mysis flexuosus is described at length, but as this account has been corrected by Bethe (**'95**), it will be referred to later in connection with Bethe's work.

The *Otocyst* (Hörblase of Hensen) is described in general as a roundish or ovoid cavity, lined with chitin; the opening, if any, is always dorsal, and varies greatly in size. It is found in the basal segment of the first antennæ of all decapods, and in the endopod of the sixth or last abdominal appendage of the schizopods. The sac is closed in the Brachiura and Schizopoda, but open in most Macrura. The otocysts of Crangon, Palæmon, Hippolyte, Mysis, and Carcinus mænas are described in more detail, but no good figures or sections are given.

Auditory Hairs or Bristles. Hensen gives the first and only good description of these. They differ from common tactile hairs in that the hair shaft is not directly connected with the wall of the sac, but a thin chitinous membrane intervenes, forming a small hollow sphere. It is this "spherical membrane" which allows the great freedom of movement necessary for the shaft in its response to sound vibrations. A peculiar process, the "lingula," projects from the inner wall of the base of the shaft into the spherical membrane, and to this the nerve fibre is attached. The hair shaft is generally plumed, as in tactile hairs, with delicate chitinous filaments.

In A. marinus the hairs are plumed and are nearly one millimetre in length. They are here very numerous, 468 having been counted in one case, and are arranged on the floor of the otocyst in four parallel semicircular rows.

A. fluviatalis has a much smaller number of hairs, but the same general arrangement; Crangon, a row of only seven or eight; these are more attenuate than in either of the above forms, but are 0.75 mm. in length.

Palæmon antennarius has about 40 hairs, arranged in a half-oval or horseshoe shape, the break in the oval being posterior. The hairs themselves are peculiar in having their shafts bent at a sharp angle. The portion of the shaft above the bend is much longer and more attenuate than the basal part, and is also heavily plumed. These plumed ends project toward the centre of the horseshoe, and intertwine. Their length is about 100 μ and their greatest diameter 3.8 μ. The hairs of Hippolyte and Mysis strongly resemble those of Palæmon, but they are embedded in the single otolith and are therefore unplumed.

Carcinus mænas has about three hundred auditory hairs. They are grouped into three classes: — 1. Hook hairs (Hakenhaare): the shaft hooked and with a plumed tip, about thirty in number, 50 μ long, similar to the otolith hairs of Macrura. 2. Thread hairs (Fadenhaare): long, filamentous, plumed at very tip, a single row of about 46, each 338 μ long, 3 μ in diameter. 3. Tuft hairs (Gruppenhaare): short, blunt, and unplumed, about 200 in number, occurring in a single large group.

Hensen also found on the appendages of some decapods free hairs which closely resembled auditory bristles, and are described as such by him. Crangon especially, which has few hairs in the otocyst, is supplied with many of these so-called "free auditory hairs." They are also numerous in Mysis and Palæmon.

Innervation of the Otocyst. In Palæmon Hensen traced the nerve of the first antenna from the brain. A large branch of this nerve runs to the ventral side of the otocyst, where the fibres separate, each enlarging into a ganglionic cell and then proceeding to the base of a hair. Each of these terminal fibres ("Chordæ" according to Hensen) then enters the pore beneath a hair, passes through the spherical membrane to the lingula, or process from the base of the hair shaft, and makes itself fast to this. In his own words (Hensen, '63, p. 368): "Dieser eigenthümliche Faden, den wir als Chorda bezeichnen, läuft eine kürzere oder längere Strecke weit bis zu einem Hörhaare hinfort, und geht durch die Mitte des Porenkanals und der Haarkugel bis zur Lingula hin, an die er sich festsetzt." Essentially the same conditions were found by Hensen in Carcinus mænas and in Mysis. He also found nerve fibres supplying the tactile bristles which are present on all parts of the decapod body.

Formation of New Hairs (Haarwechsel). New hairs are not formed inside the old, but beneath the chitinous wall; and instead of developing from a single matrix cell, as was supposed, Hensen found that each was the product of a great number of cells. A new layer of chitin is formed beneath the old, and *under* this new layer, but continuous with it, the new hairs are formed as double-walled (i. e. invaginated) tubes. The new chitin wall is compared to the hand of a glove. If the fingers of the glove be turned partially outside in, so as to leave only their tips projecting, the condition would represent that of the hair tubes just before the moulting of the old shell. The tips of the newly formed hairs become attached to the shaft of the old hair, into which they project some distance, and as the latter are detached at ecdysis, the new hairs are pulled out. Nerve fibres were found running into the very tips of the new hairs. Hensen's theory is, that at moulting, the old nerve fibre, becoming more highly refractive and resembling chitin, is, upon the detachment of the old hair, drawn out through the apex of the new one, and that before this event a new fibre is formed. This theory, however, is not easily reconcilable with his statement that the nerve fibres attach themselves to the lingula at the base of the hair shaft.

The remainder of this part of his paper is devoted to brief descriptions of the otocyst as found in some twenty-four different species of Crustacea.

To this is added a table, embracing all the forms which have been studied, giving the names of the different investigators, and the conditions, as to number and size, of both the auditory hairs proper (Otolithenhaare) and the "free auditory hairs" found on the antennæ and abdominal appendages.

Lemoine (**'68**) compares the otocyst of the lobster with that of the crayfish. His descriptions are similar to those of Farre (**'43**), but his figures are poor. The thin dorsal wall of the basal segment of the first antenna, which covers the ear sac, he calls the tympanic membrane of the lobster. The opening of the sac is overlooked, and the otocyst described as closed. Thus, as the otoliths cannot come from without, Lemoine's theory is that they are exfoliations from the calcified walls of the sac, — an absurdly impossible assumption, as the thin chitinous walls of the otocyst are not calcified. In the case of the crayfish, he notes nothing new except that there is a membrane at the base of each hair shaft, separating its cavity from that of the spherical enlargement on which the shaft stands. This membrane acts as an ear drum, taking the place of the large tympanic membrane described for the lobster.

Garbini (**'80**) discusses very briefly and incompletely the sense organs of Palæmonetes varians. The figures of the otocyst are extremely crude considering the date of the work, and simply confirm the conditions found by Hensen in Palæmon.

Vom Rath (**'87**, **'88**, **'91**, **'94**) does not make the sharp distinction between auditory and tactile hairs that Hensen does, holding that the two kinds grade insensibly into each other, the auditory hairs being simply slightly modified tactile organs. All sensory bristles of Crustacea can be divided into two chief groups: —

(1) Tactile or auditory hairs, with long, plumed shaft, the base of which is attached to the body wall by a delicate membrane of chitin, often spherical in form. Differentiation is thus towards freedom of movement in response to tactile or vibratile stimuli; (2) taste or olfactory hairs, having a short blunt shaft, thick-walled at the base, but with either a small pore or thin permeable membrane at its distal end, by means of which chemical substances in solution can come into direct contact with the nerve endings. The nervous apparatus of these hairs is the same in both cases for all decapods. The sweeping statement is made, that *beneath every sense hair there lies, either in the hypodermis, or removed some distance from it, a group of bipolar ganglion cells.* From each of these cells a fibre is given off peripherally, and these, *forming a strand, enter the base of the hair, ending only at its very tip.*

Claus ('75, '91) agrees with Vom Rath as to the nerve ending, but maintains that there is only *one* ganglion cell sending its process through a *group* of *matrix cells* into the hair. A misunderstanding as to the relations of the ganglion and matrix cells forms the basis of several controversial papers.

Retzius ('90, '92, '95) concludes in his last paper ('95) that there may be several ganglion cells to a single sensory hair. The number may indeed vary from one to many. He was unable by any method to trace the peripheral nerve fibres further than the base of the hairs. Nerve endings, which he described in his first paper ('90) as extending into the hair shaft, he afterwards ('92) frankly acknowledges to be artifacts.

Bethe ('95^a), in his admirable little paper on the otocysts of Mysis, clears up by modern methods many points, and corrects some of Hensen's erroneous descriptions. The sac in Mysis is ellipsoidal, and pointed posteriorly, while from its floor rises a sensory cushion bearing the hairs. This cushion is tilted outwards and ventralwards 45°, the right and left cushions thus being perpendicular to each other. The sac is open, not closed as described by Hensen; the narrow aperture is concealed by the overlapping walls of the otocyst. Borne on the sensory hairs is the large otolith, oval as seen from above, kidney-shaped in side view; its greatest diameter 0.3 mm., the other dimensions being 0.25 mm. and 0.15 mm. It is composed of a more or less organic core, about which concentric layers of calcium fluoride are deposited. The tips of the sensory hairs are embedded in this inorganic layer, and penetrate to the core of the otolith. The layers of calcium fluoride are probably deposited from the sea water. The sixty sensory hairs are arranged in a single row, so as to form two thirds of a circle, the break in the line being posterior and toward the median plane of the animal. At one end of the curve five hairs are grouped together, and at the other end there is an irregular double row. Though much like the auditory hairs of Palæmon, their tips, embedded in the otolith, are unplumed. Only *one ganglion cell* to a hair was found, sending a distal process into the base of each shaft. A double row of matrix cells lies just beneath the single row of hairs, and could easily be mistaken for ganglion cells. Vom Rath may have made this mistake, thus getting a multiganglion-celled condition for each hair.

The otocyst begins to develop before the appendage is fully formed. An invagination of the dorsal ectoderm takes place, producing a shallow depression; this enlarges while the opening gradually closes. Certain of the hypodermis cells elongate to form the matrix cells which later produce auditory hairs. The latter are formed only after hatching.

Herrick ('95) mentions the auditory organ only in connection with the development of the lobster. The otocyst becomes prominent at the third larval stage, appearing as a shallow depression bordered with short setæ and containing a few grains of sand. The depression gradually enlarges, forming in the fifth stage a sac, the aperture of which decreases in size with successive moults, until the adult condition is attained.

Bethe ('95, '97) has traced the auditory fibres of Carcinus mænas centrally to the neuropil of the first antenna, where they end in delicate fibrillations. Some of these fibres may also end in the globulus.

From this review of the literature, it is seen that little has been done on the finer anatomy of the otocyst. Hensen's work, once considered exhaustive, will not suffice at the present time. The organ of Brachyura has not been touched upon since Hensen's dissections, while our knowledge as to the innervation of the different sensory hairs of Crustacea is left in a very hazy, confused state, since the exact condition of the peripheral endings is not firmly established, Claus, Vom Rath, Retzius, and Bethe each holding different views. The question remains unsettled as to whether the manner of innervation is the same for all the sensory hairs. G. H. Parker ('90) has clearly shown that the optic nerve in Crustacea is highly differentiated; but all the other sense organs have, according to Vom Rath, the same manner of innervation, even though they differ in function as much as the so-called auditory and olfactory bristles.

All the investigators of the crustacean otocyst, Bethe alone excepted, carried on their work under the impression that they were dealing with an auditory organ. This certainly prejudiced them in drawing conclusions. But for this, Hensen would never have likened the thickened wall of the crab's otocysts to the malleus of the vertebrate ear, nor made other far-fetched comparisons. A comparative study of the innervation of the otocyst, especially if supplemented by that of the olfactory and tactile bristles and the conditions in embryonic stages, cannot fail to clear up some of these questionable points.

B. OBSERVATIONS.

In the account of the morphology of the otocyst, two types will be taken for description: —

(1) *Open otocysts containing otoliths* (macruran decapods); the example will be Palæmonetes vulgaris Stimpson. The otocysts of the crayfish Cambarus affinis (Say) Girard, and of the prawn Crangon vulgaris Say, will be described in only sufficient detail to allow of comparison with Palæmonetes, and to correct any errors or omissions in the descriptions of other investigators.

(2) *Closed otocysts without otoliths* (brachyuran decapods); the sac of the green crab, Carcinus mænas Lin., will be taken as the example of this type.

For tracing out the *development* of the macruran otocyst (1), young lobsters were used instead of Palæmonetes larvæ, as it is difficult to obtain a complete series of the latter, and their small size makes them by no means favorable material for studying the embryology of the sac. Young lobsters, however, can be had in abundance during the hatching season, and are of large size; the otocyst is of the same general type as that of Palæmonetes. The development of the closed otocyst (2) was traced out in the crab for the sake of comparison with the macruran type of sac.

The research represented in this paper was carried on at the suggestion of Dr. E. L. Mark, to whom I wish here to express my thanks for his constant kindness, suggestive direction, and able criticism. I am also indebted for valuable supervision and helpful suggestions to Dr. G. H. Parker, who directed my work for one year during the absence of Dr. Mark.

1. Material.

Large numbers of Palæmonetes were obtained from the Charles River, Cambridge, at low tide. These river animals live well in either salt or fresh water, and may be kept in aquaria without running water for an indefinite period. Being so hardy, and at the same time free swimmers, they are eminently adapted for *intra vitam stains*, and for physiological experimentation.

Carcinus mænas was abundant in the soft-shelled condition, at Hadley Harbor, Naushon Id., during the months of June and July. The head of Great Harbor, Wood's Hole, was another good collecting ground.

Many soft-shelled animals were obtained by keeping young crabs in aquaria, and feeding them freely until ecdysis took place.

Lobster larvæ were hatched at the U. S. Fish Commission Station, Wood's Hole, during June and July. They were reared, but with great difficulty, up to the eighth moult. Fed on minced crab's liver they throve well; but unfortunately they also fed indiscriminately on each other.

Crangon was found in large numbers in the muddy bottom of the Charles River; crayfish were bought in the New York City markets.

2. Methods.

In sectioning, great difficulty was experienced, both on account of the thickness of the chitin, which was often calcified, and because of the siliceous otoliths, so numerous in the sacs of Macrura, and glued by secretions to the hair tips. As the otoliths are insoluble in acids strong enough to completely destroy organic tissues, the only successful remedy was to remove them mechanically. This was best accomplished by washing them out by a stream of water blown into the sac. The apparatus for this consisted of a short piece of small rubber tubing into one end of which was inserted a glass tube drawn out to a fine point. The other end of the tubing being held in the mouth, and the capillary tube inserted into the aperture of the otocyst, a stream of water was driven into the cavity of the sac with considerable force. The larger otoliths having been washed out in this way, fairly good sections could be cut.

In the crab, the difficulty in cutting the very thick calcified chitin was obviated by using soft-shelled animals. The chitin is at this stage very thin, uncalcified, and therefore more readily sectioned. Lobster and crayfish antennules were decalcified by placing them in Gilson's fluid for twenty-four hours, or in Vom Rath's platinic-osmic fixative for a week or ten days.

Of the many fixing reagents used, (1) Vom Rath's platinic-osmo-picro-acetic mixture, (2) his corrosive-picro-acetic fluid, and (3) corrosive sublimate plus 1 % acetic acid gave the best results and in the order named. The last two were followed by staining in iron haematoxylin, which gave a clear definite stain of sections as thick as $20\,\mu$. The platinic-chloride fixative of Vom Rath was used for from three to five days, either followed or not by treatment with pyroligneous acid. In Palæmonetes and Crangon a fine differentiation of fibre tracts was obtained by using the fixative alone for three to five days, and washing out for at least two weeks in 90 % alcohol. The myelin sheath was intensely blackened, while all other tissues remained a yellowish brown.

For tracing nerve fibres, both to peripheral and central endings, *intra vitam* staining proved of most value. Different methods were employed for obtaining peripheral and central stains. A one per cent solution of methylen blue in normal NaCl was injected into the body in either case.

For peripheral endings several injections were made into the abdominal blood space, at intervals of thirty minutes. When the animals showed signs of stupefaction, a final injection was introduced into the pericardial chamber. The amount of solution injected varied from a few drops, in Palæmonetes, to five cubic centimetres, in the lobster. In from 15 to 30 minutes after the final injection the animals were usually dead. The part to be studied was then dissected out, barely covered with normal salt solution, and examined from time to time under the microscope, until a satisfactory degree of staining had been reached.

For central terminations one injection only was made, and this directly into the chamber of the heart, only a few drops of the solution being required. When the blue color was well diffused throughout the tissues (about one hour after injection), the brain was dissected out, or exposed, and examined as before. For fixation of the stain Bethe's ammonium-molybdate method for invertebrates was used. It was found to be better to leave preparations in xylol for only the shortest possible time, as this reagent diffuses the color. Preparations fixed by this method keep very well for a year or more, but after this they ultimately deteriorate, fibres originally sharp and continuous in outline becoming mere dotted lines, while the surrounding tissues take on a deep yellow hue. When both brain and otocyst were examined together, the peripheral cells and fibres stained first, then central fibres, central terminations, and ganglion cells of the brain in the order named. Sections 60–120 μ in thickness were cut, but by far the greater number of preparations were examined *in toto*. The transparency of the tissues made this possible even with the brains, a millimetre or more in thickness, of large crayfish.

To get constantly complete impregnations of both peripheral and central endings, it is necessary to expose to the atmosphere the part to be studied. The impregnation then takes place sooner, lasts longer, and affects a larger number of elements. The fixation of the color is also much better in this case, because the fluid can penetrate much more readily, and on the rapidity of its penetration depends, in a large measure, the success of fixation. Gold-chloride and Golgi preparations were useful only for supplementing and controlling the results obtained by methylen blue. Both the rapid and slow processes for silver impregnations gave fairly good preparations, but by no means as complete or constant results as methylen blue. Ranvier's gold-chloride method, in which formic acid is used for reduction, was very uncertain in its action on nervous tissue, but was quite useful in bringing out fine cell processes in the sensory hairs.

3. Structure and Development.

I. Palæmonetes vulgaris Stimpson.

1. *Structure of the Otocyst.*

a. Sac. This is situated, as in all decapods except the Mysidæ, in the basal segment of the antennule, nearly filling its cavity. Its outline as seen from above (Plate **1**, Fig. 1) is nearly ovate, being well rounded posteriorly, though suddenly becoming pointed at its anterior end. In individuals of medium size (30 mm. long) its average dimensions are 0.66 mm. in length, 0.63 mm. in width, and 0.33 mm. in depth. In longitudinal section (Plate **1**, Fig. 4) its outline is somewhat kidney-shaped, its length being about twice its depth, and its ventral wall projecting into the lumen. Transverse sections through the basal portion of the antennule (Figs. 2, 3) show that the lumen of the otocyst is from one half to two thirds as wide as the antennule at this point. The chitinous wall of the sac, which is extremely thin, is continuous with that of the antennule (Fig. 3). The hypodermal cells form a single layer, except in the sensory region of the sac, where they are elongate and several layers thick. Median to the otocyst passes the antennular nerve, the cut end of which is shown at *n. at. 1* (Plate **1**, Fig. 2), and directly below it lies the large muscle of the segment. Otoliths occupy the median and posterior portion of the lumen, and nearly conceal from view the sensory hairs (Fig. 3, *set. ot.*). In parasagittal sections (Fig. 4) is to be noticed the close proximity of the brain (*n' pil. opt.*), which is not more than 0.22 mm. posterior to the sac, and projects somewhat into the base of the antennule; the sensory cushion, or prominence (*crs. sns.*), bearing the stumps of a few severed hairs, is also to be seen.

The long axis of the otocyst is not coincident with that of the antennule (Fig. 1), as its anterior end is more lateral in position than the posterior. The external aperture has the form of a pointed ellipse and penetrates the dorsal wall of the antennule; it is nearly as long as the sac itself, but does not extend quite as far back as the sac. It was described by some of the early writers as a longitudinal slit, by others as transverse; but, as Hensen points out, it is neither: its direction is oblique, and corresponds to that of the long axis of the otocyst. The opening is completely covered over by a thin fold of chitin (Figs. 1, 3, *tct.*), which extends forward and laterad to end in a sharp projection or spine. This lid-like fold (tectum) must be lifted or cut away in order to come directly at the opening of the otocyst. Figure 3 shows the position and form of the lid in transverse section, and how closely it fits over the aperture of the otocyst, while its forward projection over the anterior lip of the slit can be seen in Figure 5 (Plate **2**) at *tct.* As the chitinous lining of the otocyst is of ectodermal origin, like all other chitinous parts, it is cast off at each ecdysis, with all it contains, and a newly secreted sac takes its place.

b. The sensory cushion of the otocyst is produced by an elevation of the median and posterior portion of the floor of the sac, which projects into the lumen and gives a somewhat constricted appearance to the cyst in sagittal sections. The surface of the cushion, which is about 0.25 mm. in diameter, is not horizontal, but slants downward from the median side of the sac to its lateral wall at an angle of nearly 45° (Plate **1**, Fig. 3). This makes the sensory cushions of the right and left sides perpendicular to each other, a condition similar to that described for Mysis by Bethe ('**95**^{a}, p. 556), and of some physiological importance. The sensory hairs are borne on the sensory cushion, and for this reason the prominence has been compared to the *cristæ acusticæ* of vertebrates. The hairs, or bristles (for both names are applied to them), vary from forty-five to fifty-eight in number, and are arranged in a curved horseshoe-like row (Plate **1**, Fig. 1), the two ends of which are directed obliquely caudad and mediad. Largest at the inner end of the curve, and arranged in a single row, they grow gradually smaller toward the other end of the series, where an irregular double line is formed. Fig. 6 (Plate **2**), a transverse section through the posterior ends of the horseshoe shows the base of a single hair on the right or median side, while at the left or lateral end two bristles are seen, the lateral row being double.

Directly beneath the hairs we find, instead of the usual layer of hypodermal cells, groups of cells with elongated nuclei; these send their processes into the bases of the bristles (Plate **2**, Figs. 6,7). They are the *matrix cells*, which nourish the hair and, as we shall see later, have to do with its formation. The central region beneath the cushion is occupied posteriorly by the ganglion cells of the otocyst nerve (Plate **2**, Fig. 6, *cl. gn.*), and anteriorly by their peripheral fibres.

c. Structure of hairs. The hairs of the otocyst are peculiarly modified. Instead of being straight, as in tactile hairs, the shaft is here bent out of its course about 120°, so that its distal portion makes a sharp angle with the proximal end (Plate **2**, Fig. 8). The shaft is very long in comparison with its diameter, being from 160 μ to 200 μ in length, while only 3 to 6 μ in diameter at the base. The part of it above the bend becomes extremely attenuate, and is heavily fringed with long delicate projections (pinnules), which give it the appearance of a plume. These fine feathery tips, which always project toward the concave side of the horseshoe formed by their bases, are crisscrossed and tangled together in such a way as to form a wickerlike mesh, on which the majority of the otoliths rest (Plate **1**, Fig. 3). The hairs are not attached firmly or immovably to the wall of the sensory cushion, but an exceedingly thin-walled chitinous bulb intervenes between the shaft and the wall of the sac. This, the *spherical membrane* of Hensen, is from 6 to 12 μ in diameter, and allows the shaft, itself comparatively rigid, to sway freely on its base, as if articulated there (Plate **2**, Fig. 8, *mb. sph.*).

d. The formation of hairs has already been described by Hensen (**'63**, p. 374) in some detail. The conditions just before ecdysis were figured, but the earlier stages were not given; so a few supplementary facts may be added here. Braun (**'75**) verified Hensen's account of *Haarwechsel* in the bristles of Astacus, and himself discovered some new details.

As before stated, each sensory hair is produced by a number of matrix cells, which send their processes into the shaft. In newly formed hairs, these protoplasmic processes extend to the very tip of the hair cavity (Plate **2**, Fig. 7). In preparation for the next moult they are withdrawn nearly to the base of the hair, leaving the greater part of the hair cavity empty (Plate **2**, Fig. 9). At the same time the matrix cells from which these processes are given off sink deeper into the tissue, below the level of the hypodermis, and with other chitinogenous cells originating in the hypodermis, arrange themselves about the nerve fibre of the old bristle for the purpose of forming the new hair (Fig. 9, *cl. ma.*). This aggregation of cells is similar to the *papilla* described by Braun, but they are by no means as regular in outline and arrangement as those figured by him. In Palæmonetes this condition of the matrix cells exists for several weeks before ecdysis takes place, the new hairs being formed during this period. In adult lobsters and crayfish the time is probably much longer, whereas in larvæ it lasts but a few days. The chitin of the new hair shaft is secreted *pari passu* with that of the test, so that the two are continuous, but the hew hair is *beneath* the shell, in the region where the matrix cells have formed the *papilla*. It is secreted as a double tube, the distal end of the inner part of which projects, as the tip of the new hair, into the base of the old one. Figure 10 (Plate **3**) shows the condition of affairs just before ecdysis in the endopod of the third abdominal appendage; *cta.* being the old test, *cta'.* the new one formed beneath it. Three newly formed hairs are seen as double tubes located deep in the appendage. The walls of the two tubes are continuous with each other at their lower or proximal ends, and the tip of the inner tube projects distally into the shaft of the old hair. This inner tube, the tip of the new hair, must be secreted by the delicate processes from the matrix cells which still extend up into the old hair during the period of hair formation. The outer tube, though continuous at its lower end with the inner, is secreted by two parallel rows of matrix cells, very similar to the chitinogenous cells of the hypodermis, and probably derived from them. Hensen ('**63**, p. 375) has well described this condition of the new hairs as resembling that of the finger of a glove turned partially inside out, the tips alone projecting. The tip of the new hair is embedded in a viscous, homogeneous substance, which is formed between the old and the new tests, either by glandular secretion of other cells or by the chitinogenous cells themselves. This substance probably corresponds to the homogeneous non-cellular membrane found by Herrick between the shells of the lobster ('**95**, p. 87). When the old test is shed, it adheres to the fine plumes of the new hair tip, and aided by the internal blood pressure (very considerable at the moulting period), draws the recently formed hair out into its functional position, just as one would draw out the invaginated finger of a glove by pulling on its tip. The chitin of the shaft is very soft and pliable at this time, allowing the hairs to be turned right side out with ease; indeed, this may be done artificially. But if by some accident at the time of ecdysis any of the hairs are not at once fully drawn out, the chitin hardens and they are fixed in their abnormal position.

Aside from its general interest, this peculiar method of forming the new hair is very important, as throwing light on the peripheral endings of the nerve fibres in the sensory hairs. By it certain conditions may be explained. At each moult the nerve fibres lose their connection with the old hairs, and come into relation with new ones. How these changes are brought about can best be described in connection with the innervation of the otocyst.

e. The Otoliths are borne in a rather compact mass upon the interlaced tips of the sensory hairs (Plate 1, Fig. 3, *ot'lth*). They consist of irregular grains of sand mingled with other fine mineral particles and organic detritus. The largest measure from 8 to 12 μ in longest dimension. That the greater part of them are siliceous is shown by their insolubility in strong sulphuric acid, and by the fact that they scratch glass when crushed upon it. They are renewed after each moult, for the freshly formed sac is at first without them. New otoliths are pushed in by means of the chelæ through the aperture of the sac while its walls are yet so soft and flexible as to admit quite large grains of sand. By watching animals soon after moulting it can be observed that they stir up the sand at the bottom of the aquarium in which they are confined; as soon as some particles have come to rest upon the dorsal side of the antennule, one or both chelæ are raised, and by their tips the grains of sand are pushed back under the protecting lid of the opening into the otocyst. Otocysts from which most of the sand particles had been carefully removed by forcing a jet of water into the sac were found after a lapse of two days to contain otoliths derived from iron filings which had been strewn on the bottom of the aquarium. The otoliths are often entangled in the feathery plumes of the auditory hairs, and are in this case attached to them by an organic substance, which is probably secreted by unicellular glands situated beneath the floor of the sac. No multicellular glands, such as are found in the lobster and crayfish, could be detected beneath the otocyst of Palæmonetes. Very minute canals, which are probably the ducts of gland cells, were found running through the chitin wall and some distance into the tissues beneath; they were very clearly brought out, and their tubular condition proved beyond a doubt, in silver preparations, and in those made with lead formate; but unfortunately their connection with gland cells could not be demonstrated. The functions of the otolith and the part it plays in audition, or equilibration, will be discussed in the experimental portion of this paper.

2. *Innervation of the Otocyst.*

As already noted, the brain, or supra-œsophageal ganglion, is less than a quarter of a millimetre distant from the ear sac. The nerve supplying the hairs of the otocyst is thus comparatively short, and can be traced in a single section from the central to the sensory termination. Figures 4 and 12 (Plates **1**, **3**) show its general course after leaving the brain. Its sensory ganglion lies directly beneath the posterior end of the sac. The nuclei of the nerve cells of the ganglion are situated about 0.25 mm. back of the hairs which they innervate, grouped irregularly together; the peripheral fibres of the cells run somewhat parallel to one another, then spread out radially to the different hairs of the circle which they supply (Plate **3**, Fig. 12, *fbr. pi'ph.*).

There are three questionable points to be settled in regard to the innervation of the otocyst, and the same is true for the sensory bristles of decapod Crustacea in general.

a. Is each hair supplied by one nerve fibre and sensory cell, or by many?

b. How do the peripheral fibres terminate? Do they attach themselves to a sense cell, or to some part of the hair, or do they end free? If this latter be the condition, does the fibre terminate at the base of the hair, or at its very tip?

c. Where do the fibres end in the central nerve organ, and how?

For the determination of these questions, it is important to compare the conditions found in all kinds of sensory bristles. Because different types of hairs have been used in various Crustacea for the study of the nerve terminations, and this difference in kind of material employed by various investigators may account for the very diverse conclusions they have drawn.

All sensory bristles of decapod Crustacea can be divided into two general types:

(1) *Tactile bristles* (Plate **2**, Fig. 8) have typically a long, straight, plumed, attenuate shaft, attached at the base by a thin spherical enlargement, which allows great freedom of movement.

Auditory hairs, so called, are merely modifications of these, for all gradations between the two exist. Tactile hairs are found on nearly all the appendages, and on some parts of the body.

(2) *Olfactory bristles* (Plate **4**, Fig. 13, *set. olf.*, and Fig. 14) are short, cylindrical, or slightly tapering, and firmly attached as compared with tactile hairs, there being no marked basal enlargement. At the tip, the

chitin is either pierced by a pore, or ends in a thin permeable membrane, which allows substances in solution to enter the cavity of the hair. If found on the first or second antennæ, they are termed *olfactory* hairs; when on the oral appendages, *taste* or *gustatory* bristles, though their functions are probably the same.

a. Number of Nerve Elements to a Single Bristle. Until 1891 it was supposed that only a single ganglion cell and fibre-process supplied each hair. Then Vom Rath (**'91**, p. 207) asserted, that *beneath every sensory hair of crustaceans there is a large group of ganglion cells, each sending out a peripheral process, these converging and entering the base of the hair as a single large strand.* This opinion he again expressed in 1894 for all arthropods. He did not study the innervation of the otocyst, but apparently confined his attention to the olfactory type of hair, as his figures are all of unfringed bristles.

The number of elements supplying each hair of the otocyst can be determined by, first, counting the number of fibres in the auditory nerve, and the number of nerve cells connected with these fibres, and then, secondly, comparing the statistics thus obtained with the number of hairs in the otocyst. If there is but a single cell and fibre to a hair, these numbers should coincide, at least approximately. But if there are always numerous elements, as Vom Rath maintains, then the number of fibres and nerve cells should be many times that of the hairs. The number of fibres can be readily counted in a transverse section of the otocyst nerve stained intensely with iron hæmatoxylin and only slightly decolorized. The ganglion cells can be enumerated in serial sections cut in the plane of the long axes of the cells, so that their characteristic size and bipolar condition (seen in Plate **2**, Fig. 6) will readily distinguish them from the hypodermal or matrix cells. From many such counts, the number of nerve elements was found to be approximately equal to that of the hairs. For example, in one otocyst there were 55 hairs, 53 fibres in the nerve supplying them, and 58 cells connected with these. The number of cells could not be determined with perfect accuracy, as some cells may have been halved in sectioning. Slight variations in the numbers, however, are not of great significance, as, in order to have even two nerve elements to a hair, the number of fibres or cells must be at least twice as large as that of the hairs. Moreover, the ganglion cells are always isolated, and each is surrounded by a separate sheath; their fibres are also separated from each other. Neither cells nor fibres occur in groups surrounded by a common sheath as Vom Rath (**'92**) describes them. *In the otocyst, then, there is but one nerve element to each hair.*

In the *tactile hairs* the same methods of procedure were followed; and further evidence was obtained from methylen-blue preparations. One of these is shown in Figure 11 (Plate **3**). It will be observed at once from this figure that there is only one cell and one fibre to each hair. But in other preparations of the same appendage (Plate **4**, Fig. 14) from two to ten cells are found grouped together irregularly, and sending all their processes to the same bristle. When this was the case, *it was always observed, that the hair so supplied was of the short, blunt, fringeless type,* and so possibly not a *tactile* but an *olfactory* hair.

So far, the evidence has been entirely against Vom Rath's statement; but if we examine the innervation of the *olfactory bristles*, entirely different conditions will be found to exist, and in complete accord with his conclusions.

On the inner flagellum of the first antenna of Palæmonetes numerous olfactory bristles are found, arranged in rows of four or five hairs each (Plate **4**, Fig. 13). The nerve cells and fibres supplying these hairs stain beautifully with methylen blue. Only single elements at first appear, but if the stain is allowed to act for a longer period, nearly every cell and fibre will become impregnated. It can then be seen that a large number of elements supply each hair. The cells are packed so closely together as to make the counting of a group difficult, but many counts upon sections stained in hæmatoxylin make it certain that more than a hundred cells may compose a single group, and supply a single olfactory hair. The cells send off each a peripheral fibre. These fibres enter the base of an olfactory hair as a single large strand, 12 to 15 μ in diameter. In Figure 13 only a few of the elements are shown; the sheath, which surrounds both cells and fibres, marks the outline of the spindle-shaped group of cells, and shows the size of the fibre strand.

The *gustatory hairs* on the oral appendages are also each supplied with numerous nerve elements (Plate **4**, Fig. 14). The number is not nearly so great as in the olfactory hairs, — averaging about 10 to a hair, — nor are they so regularly and compactly grouped. They differ markedly, however, from the conditions found in tactile and otocyst hairs.

The distinctly different conditions — as regards the number of nerve elements of the hairs — found in the olfactory and otocyst bristles, seem to explain the diverse conclusions of Bethe and Retzius on the one hand, and Vom Rath on the other. The two former observers worked on the tactile type of sensory bristles, while Vom Rath, as his figures show, evidently confined his attention to the other type. The conditions which

Vom Rath found in the olfactory type he too hastily attributed to all the sensory hairs of Crustacea.

b. Peripheral Terminations. Here again we find a difference of opinion. Hensen ('**63**, p. 368) asserted that the peripheral fibre was attached to a process (*lingula*) from the base of the hair shaft. Claus ('**91**), Vom Rath ('**92**, '**94**), and Bethe ('**95**) found fibres reaching to the very tip of the sensory bristles; while Retzius ('**95**, p. 17) found no evidence of nerve terminations beyond the enlargement at the base of the hair in *decapods*, though he observed in *Entomostraca* the same conditions as did the other three investigators.

I have obtained hundreds of preparations of nerve endings in the various sensory hairs of Palæmonetes with several of the best modern nerve methods, and all furnished the same evidence. The conditions found for otocyst hairs were in *every* case as illustrated in Figures 4 and 8 (Plates **1**, **2**). The ganglion cells, as already noted, lie at some distance (0.25 to 0.40 mm.) from the bases of the hairs which they supply. The reason for this becomes obvious, when the formation of the new hairs is considered. The developing hair tube extends below the base of the old hair a distance equal to at least one-third the length of the hair, and the ganglion cells necessarily lie below the lower or proximal end of the hair tube (Plate **3**, Fig. 10, *tb. set.*). Hence they must be at least a third the length of the hair distant from its base, though they occupy a closer position directly after ecdysis than for some time before. The terminal fibres (Plate **2**, Fig. 8, *fbr. n.*), which are as long as the distance of their cells from the hairs, enlarge slightly as they near their termination, and always end in the expanded base of the hair directly below the shaft proper. There are no signs of attachment to any part of the wall of the hair, nor of fine branching of the distal end of the fibre, such as Retzius ('**90**) describes. Figure 4 (Plate **1**) shows diagrammatically one nerve element of the otocyst, the position of the ganglion cell, and the ending of its peripheral fibre in the base of the hair. In Figure 8 (Plate **2**) only the termination of the fibre, highly magnified, is given.

The elements of the *tactile hairs* end in precisely the same manner as those of the otocyst. A number of these endings are shown in Figure 11 (Plate **3**). In no case was a nerve ending demonstrated in the shaft of the hair. Thus, all the evidence of preparations goes to prove that in *both otocyst hairs and tactile hairs the nerve fibre, without branching, ends in the enlargement at the base of the hair, and never enters the shaft itself.*

In the *olfactory bristles* the cells are situated about 0.45 mm. posterior to the bases of the hairs, and their peripheral nerve fibres, stained by methylen blue, were traced *in almost every preparation, some distance into the shafts,* though in the *tactile* hairs of the same appendage no fibres could be followed further than the base. Figure 13 (Plate 4) shows the olfactory endings, some of them extending half the length of the hair shaft, but *none as far as the tip;* nor was such a condition ever found, although a great number of preparations were examined. The direct evidence of preparations shows, then, that *the peripheral nerve endings are different for the different types of hairs. The fibres terminate in the enlarged base of tactile bristles, while in olfactory hairs they end free in the shaft itself.*

This direct evidence is strengthened by other structural conditions.

(1) Owing to the rigidity of the hair shaft and its delicate basal attachment, a mechanical stimulus applied to a tactile hair would be apt to produce its strongest effect at the base. Therefore we should expect to find the nerve termination at this, the point of greatest stimulation. The innervation of the tactile hairs of vertebrates extends only to the base, yet the slightest touch of the hair tip stimulates the nerve ending.

Similarly, in the otocyst hairs the point of greatest stimulation must be at the base. The hair tips are so entangled with each other, and with the otoliths resting upon them, that a stimulus applied to one must affect them all. If this stimulus is caused by the shifting of the weight of the otoliths resulting from a change in the direction of the pull of gravity, it will affect the delicate, labile articular membrane at the base of the hairs far more vigorously than the part of the shaft attached to an otolith, or entangled with the tip of another hair which is so attached.

In the olfactory hair, on the other hand, the chemical stimulus finds access through the permeable tip, and, traversing the cavity of the shaft, comes at once into contact with the terminations of the nerve, which here, as we have seen, runs some distance toward the tip of the hair. This, then, is a condition of affairs which, in view of the function of the olfactory hairs, we should reasonably expect.

(2) The *conditions during hair formation* are very unfavorable to the assumption that the nerve fibres extend to the tips of the tactile and auditory hairs. In adult Palæmonetes, a month at least before ecdysis takes place, the matrix cells withdraw their processes to the basal portion of the hair, leaving the upper part of the shaft empty. As the

shrimp moults once in two or three months, this means that for nearly half the time the nerve fibre cannot extend further than the base of the hair. Yet the animals are apparently as sensitive to stimuli during this period as at any other. After the new hair is fully formed, and its tip projects into the base of the old hair, which has now lost all direct nerve connection, the animals still respond quickly to tactile stimulus; the impulse resulting from the stimulus is transmitted from the tip of the old hair to its base, thence to the shaft of the new hair, by which in turn it is transferred to the nerve fibre.

(3) If certain of the nerve fibres supplying the tactile hairs are stained with methylen blue just before ecdysis when the new hairs are fully formed but still deeply invaginated (Plate 3, Fig. 10, *tb. set.*), they may be traced some distance into the shaft of the *new* hair. Now, by removing with a fine needle the old test, *cta.*, the new hairs can be pulled out into their functional position. The nerve fibres, however, are not pulled out with the hair the whole distance, but remain nearly in their original relative positions, barely projecting into the bases of the hairs, a condition already pointed out in Figure 11 (Plate 3).

It is unfortunate that the investigators of these nerve endings have never taken into account the tissue changes — certainly of great importance — which occur in all Crustacea between moults.

At certain stages in their formation the delicate protoplasmic processes in the tips of the new hairs stain very sharply, and have a varicose appearance, similar to that of nerve fibres; as these project some distance into the old hairs, they might easily be mistaken for terminal nerve endings.

c. Central Terminations. By means of methylen-blue preparations the nerve fibres supplying the otocyst were traced continuously in their course from the sac to their central endings. Whole preparations of the antennules and brain could be used for this purpose, as the tissues were extremely transparent. On account of the proximity of brain and otocyst, the nerve supplying the latter is very short. It enters the anterior end of the brain lateral to the antennular nerve, the two joining as they pass within (Plate 3, Fig. 12). While the antennular nerve pursues a straight course, the other (Figs. 2, 4) descends from the sensory hairs in the floor of the otocyst, forms the sensory ganglion, and in continuing its course approaches somewhat the median plane and describes the form of an elongated letter *S*, the plane of which is dorso-ventral. Just before the two nerves unite to enter the brain, a third smaller nerve is received by the otocyst nerve on its dorsal side (Plate **1**, Fig. 2, *rm. l.*). This nerve is formed by an aggregation of fibres from the tactile bristles of this segment of the antennule, and runs almost straight toward the median plane till it joins the nerve of the otocyst. The fibres of the latter enter the anterior end of the brain ventral to the optic neuropil, and median to the globulus (Plates **1**, **3**, Figs. 4, 12); they extend backward to near the posterior end of the central organ in an almost horizontal plane, lateral to the fibres of the antennular nerve. They end in a region just anterior and median to the neuropils of the second antennæ, branching into delicate dendritic fibrillæ, which form a well-marked neuropilar mass (Fig. 12, *fbr′.*).

Fibres supplying the tactile hairs of the basal segment of the antennule end in the same neuropil, while the main nerve to the antennule ends in a closely connected fibrillar mass just median to it. No nerve cells were found in the brain connected with the sensory fibres from the otocyst. Association elements, with large dendritic branches, put these neuropils into communication with the optic centres. One of these connecting fibres is shown in Figure 12 (*fbr. ass.*). Its cell, which supposably exists, was not stained. According to Bethe's (**'97**, Taf. xxviii. *an.1*) experimental work on the brain of Carcinus mænas some of the otocyst fibres should end in the globuli. He could not demonstrate such fibres, however, in his preparations of the crab's brain, nor was I able to obtain conclusive evidence of such endings in the globuli of Palæmonetes.

d. Histology of the Nerve Elements. The nerve fibres of Palæmonetes are relatively large; those of the otocyst reach their greatest size immediately before they enter the neuropil substance of the brain. At that point in their course they are from 3 to 5 μ in diameter, not including the nerve sheath. In a transverse section of the nerve the separate fibres show distinctly, as they are held apart by connective tissue.

The *fibrillar* structure was made out definitely only in methylen-blue preparations which had been well differentiated in process of fixation. The gold-chloride method of Apáthy, though tried several times, did not give a successful reaction. Fibrillæ were made out distinctly in only one preparation, though some evidences of such structure appeared in many. Figure 15 (Plate **4**) shows a portion of a peripheral fibre in which many fibrils are seen running longitudinally. No single fibril was traced any considerable distance, nor could any evidence of the fibrils be found in the ganglion cells. The fibrillæ are embedded in a semi-fluid, homogeneous substance, which is the first to take up the methylen-blue stain. It has been called by Bethe ('98) the "perifibrillar substance." The accumulation of this fluid into drops gives the characteristic beaded appearance of methylen-blue preparations.

A distinct nucleated *myelin sheath* surrounds both the fibre and the peripheral ganglion cells of Palæmonetes. This sheath, which stains intensely black in Vom Rath's platino-osmic fixative, can be traced some distance beyond the peripheral ganglion cells toward the sensory hairs, and also centrally into the brain, where it ceases only when the fibres enter the neuropil substance. Figure 16 (Plate 4) shows a ganglion cell and its peripheral process surrounded by the sheath. Elongated, flattened nuclei occur at intervals along the walls of the sheath, curved around it and the enclosed fibre; certain of these sheath nuclei can be seen in Figure 4 (*nl. tu.*) between the ganglionic cells and the brain, though the myelin sheaths are not stained in this hæmatoxylin preparation. Quite frequently one of them may occur in close proximity to a ganglion cell. Thus are produced (Plate 4, Fig. 17) appearances which might be mistaken for a ganglion cell with two nuclei. Careful study, however, shows that one nucleus (*nl.*) lies within the cell, the other (*nl. tu.*) without, but abutting on the ganglion cell so closely as to sometimes change its form. In every instance of this kind one of the nuclei, owing to its irregular outline, its smaller size, and the curved form which it takes in adaptation to the surface of the cell, could be identified as belonging to the sheath rather than to the nerve cell.

The *peripheral ganglion cells* are much elongated and are of the typical bipolar form (Plate 4, Fig. 18). They measure from 10 to $14\,\mu$ in diameter; their nuclei are relatively large, measuring from 7 to $9\,\mu$ in diameter, and are usually ovate in outline, their length in some cases being twice as great as their diameter. One large spherical nucleolus is usually present in the chromatic network, though sometimes two or more are found. No definite structure can be recognized in the cytoplasm of the cell, nor any traces of fibrillæ; this, however, is not strange, as the cell usually stains so intensely that it would not be reasonable to expect to make out its finer structure. In methylen-blue preparations a narrow zone about the nucleus stains only faintly, the coloration becoming more intense as the periphery of the cell is approached; so here, as Bethe also found in the nerve cells of Carcinus, the chromatin granules are more numerous at the periphery of the cell cytoplasm, and nearly wanting around the nucleus.

3. *Development of the Otocyst* (*in Homarus americanus Milne-Edwards*).

In order that the development of the otocyst in the lobster may be more readily understood, it may be best to compare briefly its adult condition with that of Palæmonetes.

It was dissected and described by Farre (**'43**), and again by Hensen (**'63**). The sac is drawn out posteriorly into a dorso-ventrally flattened projection, the "cochlea" of Hensen. The external aperture is extremely small, guarded by bristles, and located at the median, dorsal, and anterior end of the sac, the dorsal wall of which, like the dorsal wall of the antennule, is very thin, forming the so-called tympanic membrane. On the floor, which is nearly horizontal, there is a semi-circular ridge (Plate **5**, Figs. 24, 26), which forms the sensory cushion. From this arise the otolith hairs, which have straight shafts, and number from 500 to 600. The four rows of these are so arranged as to form a semicircle, the open side of which (at the right in Plate **5**, Fig. 26), is anterior instead of posterior as in Palæmonetes. At the anterior end of the curve there is an irregular group of smaller hairs, with bent shafts. On the median wall of the sac, near its posterior end, there is an irregular double row of long thread-like hairs, with shafts heavily fringed (Fig. 26, *set. m.*). The otoliths are numerous, and rest on the area surrounded by the rows of sensory hairs, and also on the hairs themselves; the thread-like hairs are free, and float out into the lumen of the sac.

Not much has been written on the development of the otocyst in decapods. Reichenbach (**'86**), in his work on the embryology of the crayfish, figures the invagination of the "auditory sac" at an early stage in the egg. The crayfish, however, as it develops into the adult form without passing through the larval stages characteristic of most other decapods, is not a typical example. Herrick (**'95**, p. 194) alludes to the appearance of the otocyst cavity in the third larval stage of Homarus, and he shows its position at this stage in connection with the development of the first antenna. In the fourth stage it is a shallow depression containing a few otoliths and in the fifth larva its aperture begins to close.

I shall describe its condition in the first four larval stages.

a. First Larval Stage.

(Schizopod larva, without abdominal appendages.)

Sections of lobster eggs in different stages up to time of hatching showed no evidence of the otocyst in the antennule, and it became apparent that its development took place wholly in the free-swimming stages. A transverse section through the antennule of a newly hatched larva (Plate **4**, Fig. 19) shows no sign of invagination in the region where the sac is to appear. But certain elongated nuclei, evidently those of modified hypodermal cells, are found grouped, two or three layers deep, beneath the dorso-lateral wall of the appendage (Fig. 19, *cl. ma.*). These elongated nuclei, viewed from the dorsal surface of the appendage, are seen to be roughly arranged in a semi-circle, like the rows of otocyst hairs in Figure 26 (Plate **5**), and when traced through later stages, the position they occupy is found to be directly beneath the ridge where the sensory hairs later appear (Plate **5**, Fig. 24, *set. ot.*). They are evidently, therefore, the nuclei of the matrix cells which build up by secretion the chitinous walls of the sensory hairs. These cells, like those which take part in hair formation after ecdysis, originate from the chitinogenous hypodermal cells by simply becoming elongated and sinking beneath them. A similar arrangement of matrix cells was found in the developing otocyst of Mysis by Bethe ('**95**^{a}). Numerous spherical nuclei, which stain in a manner characteristic of nerve cells, are present just below the matrix cells (Fig. 19, *n'bl.*). If traced back to the ganglionic masses of the brain, they are found to be continuous with the nerve cells of the latter, and probably originate from them.

b. Second Larval Stage.

(Second to fifth pair of abdominal appendages present.)

In this larva the first evidence of invagination is seen on the dorsal side at the base of the antennule (Plate **4**, Fig. 20). The nuclei of the matrix cells are now larger, and very conspicuous at the lateral side of the transverse section, the region where the rows of hairs will later appear. Figure 22 (Plate **4**) shows the anterior and posterior limits of the invagination and the fundament of the *sensory ridge*, marked by a fold in the hypodermis and chitin at *cl. ma.* The matrix cells just posterior to this fold, whose processes are directed toward it, are those which are to form the transverse portion of the hair rows. As in the first stage, nuclei of nerve cells lie immediately beneath the matrix cells, but the cytoplasm about them shows as yet no definite boundaries or outlines, nor are there any signs of nerve fibres connected with them.

c. Third Larval Stage.

(Chelæ relatively larger, uropods present.)

In this stage (Plates **4**, **5**, Figs. 21, 23) invagination has proceeded still further. There is a deep lateral, as well as a posterior, fold in the chitin; but the sac, if it can now be called such, is very shallow, wide-mouthed, and without sensory hairs or otoliths. From the group of matrix cells, however, the tips of embryonic sensory hairs may be made out, projecting dorsally, but covered by the chitinous floor of the sac (Plate **5**, Fig. 27). Only after the wall of the sac has been shed at the next moult will they become functional organs.

d. Fourth Larval Stage.

(Form like that of adult; thoracic exopods rudimentary.)

The sac has now greatly increased in size, and nearly fills the cavity of the appendage (Figs. 24, 25). Its opening has become smaller, and is protected by numerous fringed bristles, which project from its sides (Fig. 25, *tct.*). About 200 sensory hairs are present borne on a prominent sensory ridge (Fig. 24, *set. ot.*) and arranged in three regular rows, one row less than in the adult stage (Fig. 26). The whole band bears some resemblance to a sickle. Beginning at the median side of the sac floor, the rows curving only slightly run laterally, then with a stronger bend turn forward. At the anterior end of the sac regular arrangement ceases, the hairs being grouped promiscuously. Besides these large hairs on the sensory ridge, which measure 120 μ to 150 μ in length and from 4 μ to 6 μ in diameter, there is, as in adults, an irregular row of more attenuate hairs arranged longitudinally along the posterior part of the median wall (*set. m.*, Fig. 26). They number about thirty, are on the average 140 μ in length, and have a diameter of only 2 μ to 3 μ at the base of the shaft.

Many otoliths, consisting of fine particles of sand, rest on the hairs of the sensory ridge, as in the adult condition, but do not come into contact with the attenuate bristles of the median side-wall, which project free into the liquid contents of the otocyst. The sensory ridge is much more prominent at this stage than in the adult. This, and the size of the aperture, are the chief differences between the two, and are well shown in Figure 25. The opening gradually becomes smaller in the fifth, sixth, and seventh stages, until in the full-grown animal it is almost obliterated. A fourth row of hairs, not yet developed, is formed posterior to the others at some stage later than the seventh moult, this being the oldest stage that I have studied. Except for the gradual closure of the aperture, the larvæ of the fifth, sixth, and seventh stages show the same conditions in the otocyst as the stage under consideration.

In Figure 24 (Plate **5**) ganglion cells (*cl. gn.*) are seen beneath the sensory ridge. The origin of these could not with certainty be traced out in the material at command, though from the conditions found in the first stage, it is probable that they are derived from the neuroblast cells of the brain. The only evidence in favor of this view is the proximity of the brain, and the fact that at an early stage nerve cells which were continuous with the ganglionic masses of the brain were present beneath the matrix cells of the otocyst. Figure 26 shows, somewhat diagrammatically, the general innervation of the otocyst hairs of the fourth larval stage, as brought out by methylen blue. The condition is essentially that of the adult. There is but one nerve element to each hair, and the endings are in the enlarged bases. No myelin sheath is developed in either the larva or adult lobster. Central terminations of the otocyst fibres were not traced out, nor was their finer histology investigated.

The most striking point to be noted in the development of the otocyst of the lobster is the abrupt change which takes place after the third moult. The shallow, functionless depression of the third stage is converted at once into the active, well-differentiated organ of the fourth larva. This sudden leap in the development of the otocyst is correlated with an abrupt metamorphosis of the larva's general form and method of locomotion. As this correlation may have an important physiological significance, it will be discussed in detail in the theoretical portion of this paper.

II. Crangon vulgaris Say.

1. *Structure of the Otocyst.*

a. Sac. The otocyst has been described only briefly by Hensen ('63). He figures the sac dissected out, and gives two sketches of the sensory hairs, and the prominence upon which they are borne.

The sac, as seen in a section passing through its middle and transverse to the long axis of the antennule, has the form of a half-circle. In a cross-section more posterior its outline is made irregular by the projection of the *sensory ridge* or cushion from its *lateral wall* (Plate 6, Fig. 28). This is an entirely different condition from that found in Palæmonetes, where the sensory cushion is basal. More irregular still is its form in frontal section, as shown at *crs. sns.* in Figure 29 (Plate 6). The dimensions of the sac in individuals of medium size (25 mm. long) are:

length 0.44 to 0.55 mm.
width 0.28 " 0.38 " (anterior to sensory ridge)
depth 0.20 " 0.22 "

It is thus relatively wider, and more shallow than that of Palæmonetes. The wall is of thin chitin continuous at the large oval aperture (Plate **7**, Fig. 30) with that of the dorsal side of the antennule. The aperture is as wide and nearly as long as the sac itself; instead of a fold of chitin it has for protection a row of large fringed bristles. These are ranged close together along the posterior edge of the opening and extend their long parallel shafts beyond its anterior margin. A fine-meshed grating is thus formed, through which even microscopic organisms could not pass without displacement of the bristles.

b. The sensory cushion (Plate **6**, Fig. 29, *crs. sns.*), as already noted, projects from the posterior portion of the lateral wall of the sac. Its direction is not transverse to the long axis of the sac, but it points obliquely forward and mediad. It is a *ridge* rather than a cushion, for the hairs are arranged in a short, nearly straight single row, instead of in several rows having the form of a sickle. This row of hairs, which defines the limits of the sensory region, starting at the dorsal end of the ridge, takes a course along its convex surface downward and backward, and ends where the ridge disappears, just before the floor of the sac is reached. A portion of a row of hairs is shown in the right otocyst, Figure 29, *set. ot.* (Plate **6**), where the hairs anterior in position are really above or dorsal to those posterior to them. The ridge-like projection of the sensory prominence is best seen in a parasagittal section (Plate **7**, Fig. 30, *set. ot.*), a hair being there shown at the apex of the ridge.

The matrix cells are essentially the same as in the hairs of Palæmonetes. They occupy the region just beneath the bristles, into which their processes extend. The space in the sensory prominence below and lateral to the matrix cells is occupied by the sensory ganglion cells, the fibres from which penetrate between the formative cells and reach the bases of the hairs (Fig. 29, *cl. gn*).

c. Structure of hairs. Arranged on the sensory ridge in the manner above described, the hairs of the otocyst are 26 in number, as shown by the average of a large number of individuals. They are largest at the upper anterior end of the row, where they measure 180 μ in length and about 9 μ in diameter at the base of the shaft. Proceeding down the line they are successively smaller, the last of the series being only 100 μ in length and 6 μ in diameter. There is a conspicuous spherical enlargement at the base of the hair shaft (Plate **7**, Fig. 31, *mb. sph.*), as in the otocyst hairs of Palæmonetes. The shaft itself for about a third of its length projects straight out horizontally into the lumen of the sac. Then it bends down ventrally nearly at right angles, though the amount of curvature is different for different hairs. The larger, being in a more elevated position, usually bend at a sharper angle than those near the floor of the sac. All are heavily plumed; the pinnules are long and coarse (Plate **7**, Fig. 31, *pinn.*) and often have otoliths firmly attached to them by a substance probably of glandular origin. Hensen ('**63**) describes the otolith hairs of Crangon, as follows: "Es steht nämlich auf die schon erwähnten Vorbuchtung eine einzige Reihe von *7 oder 8* Haaren; diese Haare reichen bis zur Kugel in die Steine hinein, *ihre Zahl erscheint viel zu gering* für deren Masse. . . . Sie sind 0.075 mm. lang, 0.0075 mm. breit und gerade aufgerichtet."

This description of these hairs is completely at variance with the conditions I have found in the American Crangon. In order to determine, therefore, whether this was a true specific difference, or due to an error on Hensen's part, a number of the European specimens, procured by Dr. Mark from Professor Herdman in Liverpool, were examined. After dissecting out the otocysts of 12 specimens, I was entirely satisfied that Hensen's description was incorrect. The hairs are precisely the same in size, form, and number as in the American variety. They have their shafts distinctly bent near the tip at angles varying from 25° to 90°; of the individuals examined none possessed less than twenty-four hairs in the sac, the average being twenty-six.

That Hensen should have made such a mistake is not strange. He himself says: "their number appears much too small for the mass [of the otoliths]." The tips of the hairs are concealed by the otoliths, and only the first third of the row would be visible from above.

d. The formation of hairs after ecdysis is identical with that of Palæmonetes.

e. The otoliths are numerous, larger than in Palæmonetes, and found mostly in the posterior part of the sac, in contact with, or even attached to, the fringed tips of the hairs. Mainly siliceous, they are taken in after each moult, being readily pushed into the large opening of the otocyst. They can be almost completely washed out by a fine jet of water introduced artificially, and if the animal so treated is then placed in an aquarium containing iron filings, or other substitute, this material will soon be used to replace the otoliths of sand.

2. *Innervation of the Otocyst.*

As in Palæmonetes, the brain is very close to the otocyst, and the nerve supplying the sac is therefore short. Its general course is shown at *n. ot.* in Figure 29 (Plate **6**).

Leaving the anterior end of the brain with a bend away from the median plane, it gives off in front of the globulus a small lateral branch (*rm. l.*), which supplies the tactile bristles of the antennule. The main nerve, after passing between the globulus and the posterior end of the sac, runs forward only a short distance to the sensory prominence on the lateral side of which its ganglion lies. The peripheral fibres can be traced forward and slightly mediad from the ganglion to the bases of the otocyst hairs. The whole course of the nerve is approximately in a frontal plane, though its peripheral ending is slightly more ventral than its point of departure from the central organ. In Figure 28 (Plate 6) the transverse section of the antennular nerve (*n. at.1*) is seen to be median to the sac, while the ganglion cells of the otocyst nerve (*cl. gn.*) are lateral to it.

a. Number of Nerve Elements to a Single Bristle. There is in Crangon but one ganglion cell and fibre to each otocyst hair. The cells and fibres were counted as in Palæmonetes, and the numbers thus obtained were found to agree approximately with the number of the hairs.

Methylen-blue preparations of the olfactory nerve elements were obtained, and the conditions there brought out agreed essentially with those found in the same type of hair in Palæmonetes, large groups of nerve cells being present beneath each olfactory bristle.

b. Peripheral Terminations. Nerve fibres to otocyst hairs were never traced beyond the enlarged base of the bristle, where they end free without branching. A typical nerve element of the otocyst is given diagrammatically in Figure 29; it shows the peripheral ending of the fibre at the base of *set. ot.*

In the olfactory hairs, on the other hand, the nerve fibres in most cases could be traced up into the shaft of the hair, though never through its whole length. Thus in Crangon, as in Palæmonetes, there is a distinct difference in the innervation of the two types of bristles, both as to the number of elements, and in the manner in which the fibres end.

c. Central Terminations. Centrally the otocyst nerve ends in a position (Fig. 29) corresponding to that of the central terminations in Palæmonetes, but the fine fibrillar branching, which was brought out distinctly by methylen blue in that form, could not be impregnated in Crangon.

d. Histology of the Nerve Elements. So far as worked out, this was similar to that already described in Palæmonetes. A myelin sheath is present in Crangon as well as Palæmonetes, though it was not observed in any other decapods.

3. *Development of the Otocyst.*

This was not studied in Crangon.

III. CAMBARUS AFFINIS (SAY) GIRARD.

The otocyst of the crayfish has been figured by only Farre (**'43**) and Huxley (**'80**). The description of the former investigator was excellent for the time at which it was made. Huxley alludes to the otocyst in his work on the crayfish, and gives one figure showing the sensory region dissected out. Hensen (**'63**) describes the hairs of the otocyst in Astacus fluviatalis, but does not touch upon its other structures.

1. *Structure of the Otocyst.*

a. Sac. The otocyst of Cambarus (Plate **8**, Figs. 37, 38), except for its smaller size, resembles that of the lobster very closely. The aperture, exceedingly small in the lobster, is here quite large, though, on account of the dense *chevaux de frise* of fringed bristles, it seems smaller than it really is. These bristles, projecting from around its margin, effectually cover and conceal the opening. It occupies the middle of the dorsal side of the antennule; its anterior margin corresponds to the anterior wall of the otocyst, and it extends back from this point nearly one-half the length of the sac. Its width is about one-third that of the otocyst (Fig. 37).

The cyst does not by any means fill the cavity of the antennule. It is rounded off in front, but sharply pointed at its posterior end, where it is very shallow (Fig. 38). Its walls are of uncalcified chitin and continuous with the very thick calcified shell of the antennule (Figs. 37, 38). Its dimensions in average-sized animals are:

Length from 1.75 mm. to 2.25 mm.
Width " 1.52 " " 2.10 "
Depth " 0.85 " " 1.05 "

b. Sensory Cushion. The sensory ridge, or cushion, in the base of the otocyst is not prominent, as that part of the sac floor upon which the sensory hairs are borne is but slightly elevated above the rest (Fig. 38, *set. ot.*), and, contrary to the conditions found in the two forms already described, the sensory surface is nearly horizontal, instead of being vertical or oblique. The arrangement of the hairs is shown in Figure 40 (Plate **8**). Three sets can be distinguished, corresponding to the divisions of the otic nerve, — a median, a lateral, and a transverse or posterior. The first and third are nearly straight, the second sickle-shaped. The "median" set consists of a single nearly straight row, running from the posterior angle of the sac obliquely forward and mediad, back of which there are two or three shorter, irregular rows of scattered hairs. The lateral set consists of two concentric rows, which have the form of a crescent or the blade of a sickle, the handle of which is represented roughly by the nerve trunk connecting the bristles with the brain. The hairs of the outer row are much larger than those of the inner series. At the tip of the sickle blade the area covered by the bristles expands, and the hairs are arranged in 4 or 5 irregular rows. Behind the proximal end of this sickle-shaped double row of bristles is a short row of very large hairs, the posterior set (Fig. 40, *set. p.*), usually nine in number, which extends transversely across the posterior portion of the sac immediately in front of its pointed base. Matrix cells are found in the region directly beneath the hairs, as in the other forms described (Plate **8**, Fig. 37), and the nerve cells with their peripheral fibres lie below the chitin, either just within (lateral set), or slightly posterior to (median and transverse sets) the rows of hairs (Plate **8**, Fig. 40). By looking down upon the floor of the sac one can make out numerous small pores (represented in Figure 40 by minute circles), which penetrate the chitinous wall in that portion of the floor which is inclosed by the sensory bristles, especially in its lateral part. In transverse sections some of these pores are cut through, and it then appears that they connect with the ducts of multicellular glands which are located in the tissues beneath. One of these glands with its duct and pore is shown in Figure 39. It is apparently similar to the tegumental glands found in different parts of the lobster and figured by Herrick ('**95**, Cut 5, p. 77). In Cambarus these glands evidently supply the secretion which attaches the otoliths to the pinnules of the otocyst hairs.

c. Structure of Hairs. This has been described in some detail by Hensen ('**63**), to whose descriptions I have not much to add. The hairs are very similar in structure to those of the lobster. Their number varies greatly in different individuals, but is usually over 200. The straight, or only slightly curved, shaft is heavily fringed, and borne on the customary spherical base. Their dimensions are:

Length, from 65 μ to 175 μ.
Diameter, " 15 μ " 18 μ.

A transverse section of the shaft near its base has the peculiar shape shown in Figure 35 (Plate **7**). This modification of the form of its wall, found also in the otocyst hairs of the lobster, doubtless renders the shaft more rigid than if it were a simple hollow cylinder.

The shaft, as already noted, is nearly straight, but it is attached to the floor of the sac in such a way as to make a very small angle with its surface, being, in fact, nearly parallel to it. Thus in Cambarus the bending has taken place at the base, not, as in Palæmonetes and Crangon, in the shaft itself. In these two forms the tendency of the shaft to bend must be aided, if not caused, by the weight of the otoliths attached to the slender tips of the hairs. In the lobster and crayfish the modified form of the shaft makes it too rigid to thus give way, and the bending, if any, must take place at the thin, membranous basal sphere.

d. Formation of Hairs. (Not studied in Cambarus.)

e. Otoliths. These are composed of large grains of sand distributed mostly within the circle of hairs, and supported in part by them. As the sac has a large opening, they are readily taken in through it after each ecdysis.

2. *Innervation of the Otocyst.*

As the crayfish was well adapted for work with methylen blue, a large number of preparations of the sensory nerve elements were made, not only of the hairs of the otocyst, but also of the other sensory bristles. The nerve supplying the otocyst issues from the ventral surface, instead of the anterior end, of the brain, and at once passes forward with a slight lateral curvature to the pointed posterior end of the sac, beneath which its fibres spread out to the different hairs. It divides roughly into two strands, one of which passes obliquely forward and mediad to supply the median set of bristles (Plate **8**, Fig. 40), while the other follows the course of the lateral sickle-shaped set, lying on the concave side of the two rows, to which it gives off fibres along its whole course. Before this division of the nerve takes place, a few large fibres run out from it on the lateral side (Fig. 40) to supply the short transverse row of large bristles (Plate **7**, Fig. 33).

The sensory nerve cells lie immediately beneath the hypodermis, and their peripheral fibres run in a plane parallel with the floor of the sac. In the case of the transverse row of large hairs, the nerve cells are situated about 450 μ posterior to the bases of the shafts, their peripheral fibres being therefore nearly half a millimetre in length. This is accounted for by the position of the new hair tube during the period of its formation between moults, when it extends back from the base of the functional shaft 350 μ; the distance from base of hair to ganglion cell must consequently be somewhat greater than this.

a. Number of Nerve Elements to a Single Bristle. The number of cells and fibres for the whole sac could not be determined with exactness, as other sensory elements, supplying tactile hairs, are mingled with those of the otocyst. But in the short transverse row of large hairs, the cells and fibres are sufficiently isolated to allow of their being counted in serial sections. There are but nine hairs in that row, and if the nerve elements supplying them were twice as numerous, it would be at once apparent. The cells always occur singly, and their fibres run separately and parallel with one another to the bases of their respective hairs (Plate **7**, Fig. 33). The number of each was counted many times, and it is certain that *the number of ganglion cells and peripheral fibres exactly equals the number of hairs.* Whole preparations of these nerve elements stained with methylen blue gave regularly nine ganglion cells and fibres supplying the nine sensory hairs. In these few otocyst hairs, at least, there is, then, but a single nerve element supplying each.

In the *tactile hairs* of the scaphognathite of the second maxilla, many methylen-blue impregnations gave conditions like that shown in Figure 34 (Plate **7**), only one sensory nerve element being stained. In the short spike-shaped bristles found on this same appendage, from three to five ganglion cells (Plate **7**, Fig. 32, *cl. gn.*) were usually found supplying each bristle.

In the *olfactory bristles* of the antennule, the conditions were the same as those already described and figured for Palæmonetes, though fewer elements compose each spindle-shaped group of cells.

b. Peripheral Terminations. No branching of peripheral nerve fibres was observed in any sensory elements, though many were traced the whole length of an appendage. In Cambarus the fibres end always at the base in the otocyst hairs (Plate **7**, Fig. 33). There is often a marked increase in the diameter of the fibre near its termination, caused either by the staining of its sheath at this point, or by a partial separation of the component fibrillæ. *Tactile hairs* show similar conditions in their nerve endings (Plate **7**, Fig. 34).

The fibre strands of the *olfactory bristles* were, on the contrary, traced into the shaft some distance, where they apparently end free. Thus in the crayfish, we have a distinct difference in the innervation of the two types of sensory hairs, which serves to confirm the statements made concerning the conditions in Palæmonetes and Crangon.

c. Central Terminations. The otocyst nerve in Cambarus is large enough to be dissected out and traced to the ventral side of the brain, which it enters lateral to the larger antennular nerve. Its point of entrance is a little to one side of the median plane of the brain, opposite the posterior end of the globulus (Plate 9, Fig. 41). Its fibres run backward and dorsad, just lateral to those of the antennular nerve, and end in a neuropil directly anterior and median to that of the second antenna (Fig. 41, *n. ot.*). The individual fibres end by branching into fine fibrillations, which could be traced only a short distance through the diffusely stained mass of fibrillar tissue about them.

d. Histology of the Nerve Elements. The sensory nerve fibres of Cambarus are relatively smaller than those of Palæmonetes. Immediately after leaving the ganglion cell each measures about $3\,\mu$ in diameter, but becomes smaller as it runs distally, until near the point of ending, where it again enlarges to its original size. In well differentiated methylen-blue stains, fibrillar structure is clearly brought out. Longitudinal sections, and whole preparations of continuous fibres, show fibrillations similar to those figured for Palæmonetes.

The sensory nerve cells are relatively large; they measure from 15 to $18\,\mu$ in diameter, and being bipolar are spindle-like in form. Their nuclei are spherical and from $10\,\mu$ to $12\,\mu$ in diameter. The cytoplasm of the cell never shows any evidence of fibrillations, but in methylen-blue impregnations there is a faintly staining zone directly about the nucleus; the remainder of the cytoplasm takes on a deep blue color. This difference in staining qualities may be due to the unequal distribution of chromatic substance in the cytoplasm.

The myelin sheath, so characteristic for the nerve fibres of Palæmonetes and Crangon, is not found in the nerve elements of the crayfish.

3. *The development of the otocyst* was not studied in Cambarus. According to Reichenbach ('86) it is completely formed before the young animal leaves the egg.

IV. CARCINUS MÆNAS LEACH. (*Green crab.*)

We now come to the second type of otocyst, which is found in all brachyuran Crustacea; it is closed, and without otoliths. Mistaken by Bate ('58) for an olfactory organ, and figured by him in the larval stages of the crab, it has been described carefully in Carcinas mænas by Hensen ('63) alone. His account, although fairly accurate, is influenced by his seeing a fancied resemblance between the otocyst and the vertebrate ear; the figures he gives of different parts of the sac dissected out leave one somewhat in the dark as to the relative positions of the structures described.

1. *Structure of the Otocyst.*

a. Sac. The basal segment of the antennule in Carcinus is relatively large, and elongated laterally to such an extent that its width is nearly twice its length (Plate **9**, Fig. 46). Along its dorsal wall there extends transversely a distinct line dividing the chitin of the anterior part of the segment (*lab. a.*) from that of the posterior. This line of division, which reaches from the lateral margin of the segment three-fourths of the way across its dorsal wall, is rendered more prominent from the fact that the chitin posterior to it (*lab. p.*) is much lighter in color than that in front.

If the antennule of a crab is examined directly after ecdysis, when the chitin is still very thin, soft, and uncalcified, this lighter colored area (Fig. 46, *lab. p.*) is found to be a fold, projecting forward over the anterior part; and if its edge is lifted with a needle or fine pair of forceps, a transverse aperture is disclosed leading down to the lumen of the sac. This aperture extends from line 45 (Fig. 46) laterally down through the side wall of the antennule. There is, then, in fact, a free passage into the otocyst directly after moulting, a condition necessitated by the casting off of the old sac. But almost immediately after ecdysis, the opening is closed and its edges fuse together, probably owing to the simultaneous secretion of chitin by the hypodermis of the two surfaces which bound the orifice and are in direct contact. Figure 44 (Plate **9**) shows at *lab. p.* the two surfaces which fuse.

The form of the sac is very irregular, so much so that Hensen despaired of describing it. Its walls, like those of the forms already studied, are continuous dorsally with the calcified chitin of the antennule (Figs. 42–48, Plate **9**). The sac is thus suspended from the dorsal wall of the appendage. Although composed largely of thin chitin, one portion of its wall is much thickened and calcified (*mal.*, Figs. 43–48, Plate **9**). On account of its irregular outline measurements can be of only small value. The average of a number of measurements taken of the otocyst in specimens approximating 30 mm. in length, gave the following results: —

Greatest length, 1.11 mm.
" width, 1.96 "
" depth, 1.05 "

The seemingly contorted shape of the sac is caused by three protuberances or invaginations of its walls, which project into the lumen (Fig. *A*, and Plate **10**, Fig. 55). Two only of these prominences are sensory and bear bristles (Fig. *A*, *set. ta.* and *set. fil.*). The third and largest of the three (*mal.*), which projects from the lateral and posterior wall of the cyst, is without sensory organs of any kind. Its wall is irregularly curved and pitted (Plate **9**, Fig. 47 *mal.*,), while portions of it are even calcified. At one point its walls are constricted to form a neck, which bears a large hammer-like head (Fig. 47). This is the "Hammer" of Hensen, compared by him to the malleus of the vertebrate middle ear. Figures 43, 48, and *A* show the relative position of this hammer to the rest of the sac. It serves merely for the attachment of the short, thick, powerful muscles of the antennule which keep the latter in almost constant motion, and has probably nothing whatever to do with the sensory functions of the otocyst.

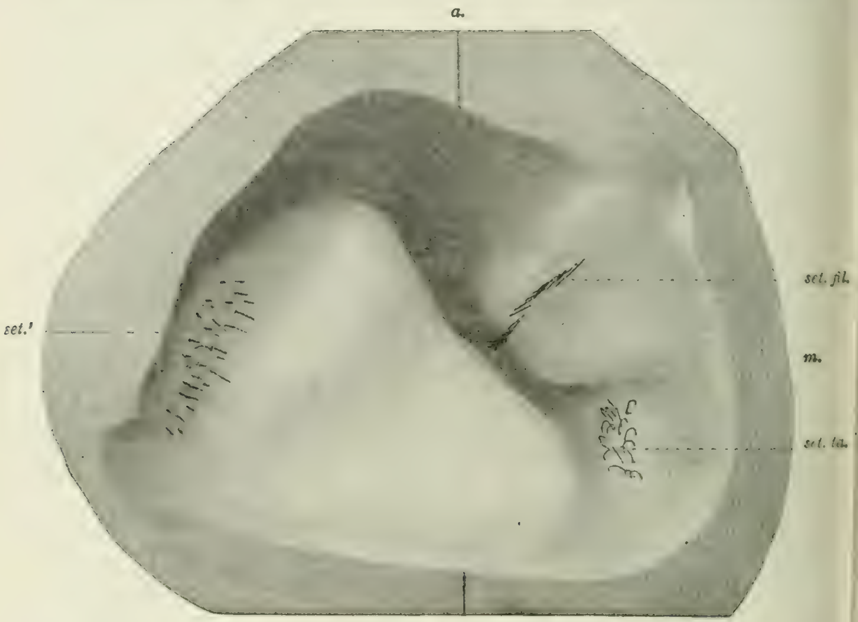

FIGURE *A*.

Model of the lumen of the left otocyst of Carcinus, dorsal view, the upper wall of the sac removed. The cavity of the sac was modelled in wax from serial sections under a magnification of 50 diameters, and a plaster cast of the model photographed natural size. In making the cut this was reduced to a magnification of 33 diameters. *a.*, anterior; *m.*, median; *set.'*, group hairs; *set. fil.*, thread hairs; *set. ta.*, hook hairs.

b. Sensory Cushions. Of the three projections noted, the remaining two are sensory and bear sensory hairs (Plate **10**, Fig. 55, *set. ta.*, *set. fil.*). The smaller of these (*set. ta.*), located on the median portion of the posterior wall of the sac, bears a number of hairs with hooked shafts. The surface bearing these lies in a nearly vertical plane. From its position and the shape of its hairs this prominence is comparable to the sensory cushions upon the surfaces of which the otoliths are lodged in Palæmonetes, Crangon, and the crayfish. Irregularly disposed matrix cells are situated in clusters immediately beneath the hooked hairs (Plate **10**, Fig. 50), and deeper in the tissues are the ganglion cells of the nerve fibres which supply the bristles (Fig. 50, *cl. gn.*). In the larval stages of the crab this sensory cushion is relatively much larger. It extends through half the length of the sac, and its hairs are in contact with the otoliths which the sac then contains. Pores of tegumental glands penetrate the chitin of this prominence, as they do that of the sensory cushions in the crayfish and lobster, although found in no other part of the sac. These glands secrete a substance which, in the larval crab, attaches the otoliths to the tips of the hairs. Their presence in the adult crab is evidence in favor of the homology of this cushion with that described for otocysts containing otoliths.

The other sensory cushion is much larger, and is produced by a partial invagination of a portion of the median and anterior walls of the sac, which forms an oval prominence (Fig. *A;* Plate **9**, Fig. 48; Plate **10**, Fig. 55, *set. fil.*). It is nearly 0.5 mm. in diameter, and its surface, making an angle of about 45 degrees with both the transverse and sagittal planes of the animal, inclines backward, inward and downward (Plate **9**, Fig. 45). Its ventral portion is shown in transverse section in Figs. 47 48. The chitin of this cushion is very thin; upon it is a row of long delicate hairs, called by Hensen ('**63**) "Fadenhaare," or thread-hairs. This row runs down somewhat obliquely from the upper side of the prominence to its ventral margin near the floor of the sac, its dorsal end being the more anterior of the two (Fig. *A*, *set. fil.*).

This sensory cushion is also found in the sac of the larva, and the bristles it then bears are similar to those found projecting free into the lumen of the lobster otocyst from its median wall (Plate **5**, Fig. 26, *set. m.*). The prominence we are now describing in Carcinus is probably therefore simply a further differentiation of the slight projection noted in the sac of the lobster.

Matrix cells send delicate processes into the hairs, as in those of preceding species; the ganglion cells are situated directly beneath the hypodermis, but some distance posterior to the bases of the hairs (Plate **10**, Fig. 53, *cl. gn.*).

No gland pores are present, nor are they needed, as the thread hairs are never in contact with the otoliths, even in the larval stages.

A third region, on which sensory hairs are located, is found at the extreme lateral side of the sac, beneath the fused lips of its opening (Fig. *A*; Plate **9**, Fig. 42, *set.'*). There is only a slight prominence, the surface bearing the hairs being nearly flat. The hairs are arranged in irregular fashion, somewhat like the groups of otocyst bristles situated near the aperture of the sac in the crayfish and lobster. Numerous groups of matrix cells lie directly below these hairs, but no nervous structures could be distinguished in their vicinity.

The great hammer-like prominence, which serves for the attachment of the antennular muscles, separates the sac roughly into an upper, anterior chamber and a lower, posterior one. The first of these compartments is again partially separated into two by the anterior sensory prominence, which nearly meets the "hammer." These three chambers, into each of which sensory hairs project, were likened by Hensen to the semi-circular canals of the vertebrate ear, and the sensory regions to the *cristæ acusticæ.* As the compartments are in free communication, are not at all canal-like in form, and are arranged in no definite positions relative to each other which might be of functional importance, there seems to be no more logical reason for making such a comparison than for comparing the hammer-like projection of the otocyst to the malleus. The apparent division of the otocyst into three compartments is not a modification for the purpose of increasing its usefulness as a sense organ, but evidently a condition brought about mechanically by the differentiation of the "hammer" along lines which would make it better adapted for the attachment of muscles.

c. Structure of Hairs. The hairs, as already indicated in describing the sensory regions, are of three kinds. Hensen's account of them is fairly good. He divides them into the following classes: (1) hook hairs (Hakenhaare), (2) thread hairs (Fadenhaare), and (3) grouped hairs (Gruppenhaare).

(1) *The hook hairs* are found on the posterior vertical cushion (Fig. *A* and Plate **10**, Figs. 50, 55, *set. ta.*) arranged in a very irregular curved row. They vary from 25 to 31 in number, and are relatively very small, averaging 49 μ in length and 4 μ in diameter. Their shafts are hooked, often bent nearly double, and are sparsely fringed near the tip, if at all. The base is enlarged, as is usual in otocyst hairs, but not so markedly as in the forms already studied. Instead of being attached to a large spherical membrane, the base of the shaft is set

into a cup-shaped depression and so labilely fastened to the chitin of the sac wall (Plate **10**, Fig. 51) that the hair can sway freely in any direction, as if it were attached by a ball-and-socket joint. This cup-like depression is characteristic of all the otocyst hairs of Brachyura.

The hook hairs are present in the otocyst of the Megalops larva of Carcinus, and are there relatively much larger; they extend over a large portion of the posterior end and floor of the sac, the curved row of 25 to 30 hairs occupying two-thirds of its length. As the otocyst is open at this stage, it contains numerous otoliths, and these are either *in contact with, or attached to, the tips of these hairs.* Measurements of a number of these larval hairs were made in the Megalops and the stage succeeding it, and a comparison of these with the same hairs of adults is made in the following table:

STAGE.	Width of Otocyst.	Average Length of ten Hook Hairs.	Average Diameter of ten Hook Hairs.
Adult (30 cm. long)	1.96 mm.	49 μ	4 μ
Young crab	0.24 mm.	47 μ	4 μ
Megalops larva	0.21 mm.	46 μ	4 μ

This table brings out the interesting fact that the hook hairs of a Megalops larva, of a young crab and of an adult are of nearly equal size, although the otocyst of the adult is nearly ten times as long as that of the Megalops, and over eight times that of the young crab. On measuring the thread hairs to see if the conditions there were the same, it was found that in the adult they were three and a half times as long as in the Megalops stage; the thread hairs thus more than tripled their length, while the hook hairs remained constant. The number of hook hairs is approximately the same in the Megalops otocyst and in the sac of the adult. Their arrested development may be explained by the fact that they are true otolith hairs; when the otocyst becomes permanently closed, otoliths can no longer enter the sac, and these hairs, as they lose their original function, do not grow *pari passu* with the other hairs of the otocyst, but remain unchanged. They do not degenerate and become entirely functionless, for they are still innervated in the adult crab, and, though sac after sac is shed and new ones formed without an otolith's finding its way into the organ, they still retain the peculiar form of the original otolith bristles.

We are thus led to regard the hook hairs of the crab as homologues of the otolith hairs of Macrura, and for these five reasons:— (1) The similarity in their structure. (2) Their similarity in position at the posterior end of the sac. (3) Otoliths are in contact with the hook hairs in larval stages, though not in the adult. (4) When the otoliths disappear, the development of the hook hairs is arrested. (5) Gland pores open through the chitin of their cushion, as they do through that of the crayfish and lobster, although they are not found in the other sensory regions of the sac.

(2) *The thread hairs* are the largest, the most highly differentiated, and probably the most active sensory bristles of the otocyst. There are about thirty of them, arranged upon the large anterior sensory cushion in a regular row (Fig. *A, set. fil.*). These hairs are extremely attenuate. Measuring only two or three μ at the base, the straight or slightly bending shaft averages $320\,\mu$ in length; it is unfringed save at the very tip, where for a short distance it bears two rows of extremely delicate pinnules. A peculiarity of this fringed tip is that it is not a continuation of the main shaft of the hair, but seemingly a diminutive hair in itself, sprouting from the latter. It makes a slight angle with the main shaft, the end of which projects a short distance beyond the base of the offshoot (Plate **10**, Figs. 53, 54). The shafts of these hairs are directed out laterally, and slightly posteriorly, into the fluid contents of the sac, and they are so delicately attached at their bases that the slightest jar imparted to the liquid in which they float is sufficient to set them swaying. In alcoholic material they break off very easily. The shaft decreases somewhat in diameter towards its base and then suddenly enlarges. This enlargement is attached to the floor of a deep cup-like socket, the orifice of which is large enough to give ample play to the shaft in its movements (Fig. 53).

Straight attenuate hairs are found in the otocyst of the Megalops larva having the same relative position in the sac as the thread hairs of the adult. These hairs are not in contact with otoliths, but each shaft is fringed with filaments throughout its whole length. They become differentiated in later stages into the peculiarly modified thread hairs. Hairs similar to those of the Megalops larva just described are also found in the otocyst of the adult lobster, situated on the median wall of the sac and projecting free into its lumen. They are similar in both larva and adult, and are probably in function accessory to the otolith hairs. They may be homologues of the thread hairs.

which, in the crab, with the disappearance of the otoliths, have taken on the chief functional activity of the otocyst, formerly vested in the hook hairs.

(3) *The group hairs* (*set.'*) form the third and most numerous class of the otocyst bristles of Carcinus. Irregularly distributed in the most lateral corner of the sac (Fig. *A*,) on a flattened portion of the wall ventral to the closed margins of the aperture (Plate **9**, Figs. 42, 47; Plate **10**, Fig. 55), they are unlike any of the otocyst hairs found in Macrura, being short, thick, and blunt, without a trace of fringing filaments (Plate **10**, Fig. 49). They are 110 μ to 135 μ long and 12 μ to 14 μ in diameter. There are nearly 200 of these hairs, forming one large irregular group. They do not occur in the Megalops otocyst, therefore they must be developed at some later period. They may possibly be degenerated tactile hairs which in the formation of the otocyst have been folded into its cavity. Their proximity to the aperture of the otocyst makes this supposition highly probable. Their shafts are set into depressions in the sac wall, and, like the other otocyst hairs, they can sway freely on their bases.

d. Formation of Hairs. The hairs are formed in Carcinus, and in the Brachyura generally, after the method already described in Palæmonetes. From the presence of a cup-like depression at the base of each shaft, instead of the large spherical membrane found in the Macrura, it might be inferred that the cup results from the incomplete evagination of the hair.

e. Otoliths are entirely wanting in the adult otocyst, but are present in those larval stages where the sac is still open. They consist, as usual, of grains of sand, which in this case are very small, for the sac itself in these stages is less than 0.3 mm. in length. They can readily be introduced into the otocyst of the Megalops, as its aperture is relatively large. When in a succeeding stage the sac is cast off with its otoliths at ecdysis, the aperture of the new cyst closes at once, and no foreign particles can enter it; henceforth it is without otoliths.

2. *Innervation of the Otocyst.*

The general course of the otocyst nerve is shown in Plate **10**, Figure 55 (*n. ot.*). As in the forms previously described, the sac lies in close proximity to the brain, and its nerve is consequently short. It is given off with the antennular nerve from the anterior end of the central organ, and its course for a short distance is directly lateral, until the base of the antennule is reached. At this point the antennular nerve (*n. at.1*) turns straight forward, while that of the otocyst divides into three branches (Fig. 55, *n. ot.*, *n. ot.'*, *n. ot.''*). The most median and largest of these runs forward to supply the thread hairs; the middle branch goes directly to the posterior sensory cushion, which bears the hook hairs; while the third and lateral offshoot takes a nearly straight course along the posterior wall of the sac and supplies the tactile hairs of the antennule, and possibly the group hairs of the otocyst. The ganglion cells of the hook hairs are some distance posterior to the hairs and arranged in an irregular scattering group (Plate **10**, Fig. 50, *cl. gn.*). Those of the thread hairs are lateral and posterior with reference to their hairs, lying immediately beneath the hypodermal cells of the sensory cushion, and forming an irregular single row, which is nearly parallel to the row of thread hairs (Plate **10**, Fig. 53, *cl. gn.*).

a. Number of Nerve Elements to a Single Bristle. The nerve elements of the thread hairs were brought out clearly and completely by methylen blue and by Vom Rath's platinic-chloride method. The conditions found in a number of preparations are shown in Figure 53, where there is but a single element for each hair. This particular preparation was obtained with methylen blue, but the results were verified by Vom Rath's method. Counted in serial sections, the number of hairs and ganglion cells were approximately equal.

By the same method of counting, the elements of the hook hairs gave like results. In one case there were thirty hairs and thirty-one cells. No ganglion cells could be made out near the group hairs, nor any fibres supplying them. Certain clusters of cells are found directly beneath their bases, but their large peripheral processes, irregular outlines, and lack of central fibres marked these as matrix rather than nerve cells.

Here in Carcinus, then, as in the macruran forms described, *there is but one nerve element to each otocyst hair.*

The distal segment of the antennule was by chance sectioned in making preparations of the otocyst, and when stained with iron haematoxylin, the innervation of the *olfactory* hairs found in that region was sharply brought out (Plate **10**, Fig. 52). As in the examples of this type of hair already described, a large spindle-shaped group of about 100 ganglion cells sends a strand of nerve fibres to the base of each shaft. These cells are relatively small and situated 0.5 mm. posterior to the hairs they supply. In Figure 52 a single nerve element is shown diagrammatically in black.

b. Peripheral Terminations. As seen in Figure 53 (Plate **10**), the terminal fibres going to the thread hairs enter the pore at the base of the cup-shaped depression, pass up into the enlargement of the hair shaft, and there end free. In fact, there is in these hairs no functional necessity for the further continuance of the fibre into the shaft. Since the hairs project free into the liquid of the sac, if the otocyst is jarred or tilted, the shaft does not itself bend, but sways backward and forward upon its base. It is therefore at the base that the stimulus must manifest itself, and it was there in every case that the fibres were found to end.

In the olfactory hairs, on the other hand, the nerve fibres continue up into the large hollow shafts for some distance (Plate **10**, Fig. 52, *set. olf.*). The olfactory hairs of Carcinus thus differ in their innervation from those of the otocyst, both *in the number of nerve elements* supplying each hair, and *in the peripheral nerve endings.* In the bristles of the otocyst there is but a single nerve element, and it ends free at the base of the hair without branching. In the olfactory hairs there may be a hundred elements or more which end in the shaft of a single hair.

c. Central Terminations. Entering the brain in front of, and just median to, the globulus, and ventral to the optic centres, the fibres of the otocyst nerve run straight back and enter the fibrillar mass (Plate **10**, Fig. 55, *n'pil. at.1*), called "the neuropil of the first antenna" by Bethe (**'97**), who has described the central endings of the antennular nerve of Carcinus. The fibres of the antennular nerve end in a connected neuropil just median to those of the otocyst. Bethe judged from his physiological experiments that there should be certain fibres from the otocyst ending in the globulus. He was not able to demonstrate such endings with methylen blue, nor was there any evidence of their existence in my preparations. According to Bethe the fibres from the otocyst end by the separation of their fibrillæ in the neuropil. Lack of fresh Carcinas material prevented the verification of his work, but I have described similar conditions in the shrimp and crayfish.

d. Histology of the Nerve Elements. As the finer structure of the elements of the central nervous system has been fully described by Bethe (**'98**), it is unnecessary for me to say anything on that matter, and only a few words need be added here as to the histology of the peripheral nerves and cells. The peripheral nerve fibres are much smaller than in Palæmonetes or Crangon, and are without a myelin sheath. The peripheral ganglion cells are relatively large, averaging 12 μ in diameter. They are of the typical bipolar form, and are much elongated (Plate

10, Fig. 50, *cl. gn.*). Their nuclei are nearly spherical, and contain at least one large deeply staining nucleolus. No special preparations were made for the purpose of demonstrating fibrillæ in either nerve cells or fibres. Bethe found them in all fibres, and traces of them in the cells of the brain.

3. *Development of the Otocyst.*

For the purpose of comparison with development in the lobster, the antennules of the first five free swimming larval stages of Carcinus were dissected out, stained and examined *in toto*. By this means it was ascertained that *there is no functional otocyst in the Zoea stages.*

(*a*) *The first Zoea* shows no trace of invagination in its antennule. There is, however, an aggregation of nuclei beneath the chitin of the region where the otocyst is to appear.

(*b*) *The second Zoea* shows a slight depression on the dorsal side of the antennule, and its basal portion has begun to widen.

(*c*) *In the third Zoea* this widening has increased, and the lateral wall of the antennule has now formed a rounded protuberance. The invagination has increased in size and depth, but no hairs nor otoliths are yet contained in it.

(*d*) At *the Megalops stage* we find that a sudden development has taken place, as in the fourth larval stage of the lobster. The Zoea has by a single moult become metamorphosed into a Megalops, and the otocyst changed from a shallow depression to a nearly closed sac, containing sensory hairs and otoliths. Two sensory cushions are present: one of these, posterior and median, bears 25 to 30 hooked hairs, upon the tips of which otoliths rest; the other prominence projects from the anterior portion of the median wall, and bears a vertical row of about 30 hairs, the shafts of which are directed laterally. These hairs are long, attenuate, and well fringed with delicate filaments. They do not come into contact with the otoliths, and, as already noted, they develop into the thread hairs of the adult; those of the first sensory cushion described correspond to the hook hairs of the mature crab. The third type of hair found in the adult is not developed at this stage. The aperture is anterior and lateral in position, and extends transversely across the antennule.

(*e*) The next stage examined was that of a young crab probably of the stage immediately succeeding the Megalops larva. The otocyst is slightly larger, and its opening is already nearly closed. As a result, only a few small otoliths were contained in it.

The otocyst of Carcinus thus resembles very closely in its development that of the lobster. In both there is no trace of the organ in the newly hatched larvæ, and for three successive moults it is not functional. In the fourth larval stage, with a sudden metamorphosis of the animal's general form, the otocyst is also rapidly changed from a mere depression to an active, well-developed organ. The significance of these sudden correlated transitions will be seen when the otocyst is considered physiologically.

C. THEORETICAL CONSIDERATIONS.

1. Comparison of the Otocyst with the Vertebrate Ear.

The otocyst has been compared by many investigators to the auditory organ of vertebrates. Leaving their functions entirely out of account, how far do the two correspond in structure?

The otocyst of Macrura consists of an open sac, a sensory prominence, bristles, and otoliths resting upon them; essentially the same conditions as are found in the ear of Myxine, though the latter has five sensory regions instead of one. The otocyst of macruran decapods might thus be well compared to an isolated ampulla in the ear sac of Myxine, and the sensory cushion to a single crista acustica.

In the Brachyura the organ is still more highly differentiated. The sac is closed, there are three sensory regions, and the hairs found on them project free into the lumen of the otocyst; otoliths are entirely wanting. The structure of the sensory apparatus is in this case similar to that of the cristæ of higher vertebrates, and the sac itself resembles the utriculus. But *there is no portion of the decapod otocyst so differentiated as to bear more than a fancied resemblance to the semicircular canals, the middle ear, or the cochlea of higher vertebrates.*

Each crista acustica in vertebrates, however, is made up of separate elements, which may be compared to the sensory elements of the otocyst. Every auditory hair of the crista is developed from the exposed end of a specialized epithelial sense cell, which itself forms the basal part of the hair, and is supported in position by the other cells of the epithelium. It has been shown by both Retzius ('94) and Morrill ('98) that these epithelial sense cells of the cristæ in vertebrates are not true nervous elements, as the auditory fibres are not continuous with them. Both the cell and its auditory hair taken together are to be compared to the bristles of the otocyst, in that they constitute a non-nervous end-organ.

Their innervation is also essentially the same. In the vertebrate crista an auditory nerve fibre passing from the brain is connected with a bipolar nerve cell in the auditory ganglion, from whence its peripheral fibre extends to one of the epithelial sense cells, ending with a slight enlargement in close proximity to, or in contact with its base. *The single fibre supplying each end-organ is never directly connected with the cell, nor does it ever run through it to the hair itself.* The only difference between the peripheral endings just described, and those of the otocyst, is that in the hairs of the latter the fibres end free in the base of the hollow shaft, at the point where, from the structure of the hair, the greatest stimulus would be produced ; while in the vertebrate end-organ the nerve process is applied to the convex under-surface of the basal cell, which would transmit stimuli with an equal degree of intensity to fibres in contact with it at any point.

The otoliths of the vertebrate ear are formed by secretion, while those of the crustacean otocyst are largely granules of sand taken into the sac from the exterior. In some Crustacea, however, such as the Mysidæ, and in many other invertebrates, the otoliths are formed within the sac.

In all decapods the innervation of the otocyst hairs distinctly differs from that of the olfactory bristles, not only as to peripheral terminations, but also in the number of nerve elements supplying each hair. As has been previously noted, the stimulus is transmitted by specialized cells or hairs to the nerve fibres of both the otocyst and the vertebrate ear, and is never applied *directly* to their endings. In either case *only one nerve element* is usually in contact with the terminal sense cell, and this is apparently ample to carry the isolated nervous message to the brain. With the olfactory sense it is different ; in both vertebrates and Crustacea the chemical stimuli which produce the olfactory sensations act directly upon the nerve cells or their terminal fibres. In vertebrates portions of the nerve cells are exposed at the surface of the olfactory epithelium. In crustacea peripheral fibres from the ganglion cells of the olfactory nerve end free in the hollow, perforate bristles. In Nereis and the earth-worm, Langdon ('95, '00) has shown that the processes of the olfactory cells end free upon the surface of the cuticula, and completely exposed to chemical stimuli ; a similar condition has been shown by Lewis ('98) to exist in two polychætous worms of the family Maldanidæ.

The large numbers of nerve elements ending in each olfactory tube or bristle of decapod Crustacea may be accounted for by the fact that the stimulating chemical substances occur as slight traces only. In order that a sensation may be perceptible, apparently a large number of olfactory elements must be stimulated at once, for the larger their number, the stronger should be the sensation produced. The olfactory bristles are located on the flagella of the antennules, a position most favorable for the reception of chemical stimuli, as the flagellum projects some distance in front of the animal and can be kept in constant motion. The number of the bristles is limited on account of the small surface to which they are necessarily confined, so that, if thousands of olfactory fibres are to function simultaneously, large numbers of them must be exposed to the chemical stimulus in the same hair. It is possible, too, that different nerve elements may be affected by different substances in solution; and that consequently many olfactory elements are necessary for each hair, in order that different chemical stimuli may be perceived.

2. The Neuron Theory.

The conditions found in the sensory nerve elements of the otocyst are favorable to the neuron theory, in so far as they confirm the generally accepted idea that the nerve fibres are each differentiated from a single nerve cell, and that fibre and cell taken together form a trophic unit. This conclusion is borne out not only by the structural conditions already described, where each fibre is connected with only one peripheral ganglion cell, but also by an experiment which I made by severing the otocyst nerve proximal to its ganglion; in this case after the lapse of a few weeks degeneration of the sensory fibres took place back into the brain.

As to the modifications of the neuron theory recently proposed by Apáthy (**'97**) and Bethe (**'98**), — that the neurons are connected by fibrillæ, — the fibrillar structure of the fibres is confirmed by my preparations, though no fibrillæ could be demonstrated in the nerve cells. In regard to the definite connection of the neurons with each other by continuous fibrils, such as Apáthy figures and describes in the Hirudineæ, my preparations gave no positive evidence; but the fact that the central fibrillations of the nerve elements of the otocyst could not be traced to determinate endings, makes it quite possible that such a direct communication between motor and sensory neurons may exist. While Bethe proved that there were more fibrillæ in a motor fibre than extended into its central ganglion cell, and also, that some fibrillæ entered the fibre by one branch and at once passed out by another, in no case did he trace a single fibril from one neuron into another. If such a connection between nerve elements had been demonstrated beyond a doubt, they might still be considered as distinct trophic units, and the interdigitating fibrils uniting them as the products of separate neuron cells. In the light of the important discoveries of Apáthy and Bethe, however, the old view, that the nervous impulses are transmitted from sensory to motor neurons by the simple contiguity of their dendritic processes, may have to be abandoned for the more reasonable assumption of direct fibrillar communication.

PART II. — PHYSIOLOGY.

As Bethe has well said, the best of anatomical knowledge concerning an organ cannot be taken as certain evidence of its functions. It is only after these functions have been experimentally demonstrated, that we may ascribe them with confidence to the organ in question.

Have we, then, any experimental proofs that the decapod Crustacea hear? If so, is the otocyst the auditory organ; if not, what is its function? These are the three chief questions which I shall attempt to answer.

A. HISTORICAL SURVEY.

Up to the time of Delage (**'87**) the auditory function of the otocyst was accepted, and that alone.

Minasi (**1775**) promulgated the idea that Crustacea could hear. The hermit crab, Pagurus, was more sensitive than man to sound vibrations. The tones of a distant bell, the striking of a clock, were, according to this worthy monk, perceived by Pagurus sooner than they were by him.

Ælianus (**1784**) notes that the fishermen of his time took Pagurus by means of music.

All the older zoölogists have regarded the otocyst as an organ of audition.

Hensen (**'63**) was the first to get experimental data. From the anatomical conditions found in the otocyst of the lobster, he argues as follows: Here are 468 auditory hairs upon which otoliths rest. Of these hairs no two are of the same size; they vary in a nearly continuous series from 0.72 mm. to 0.14 mm. in length; thus the volume of the largest is to that of the smallest as 140 : 1. Comparing these ratios to those of the volume of organ pipes, we should have, *if the hairs responded to different sound vibrations*, an auditory organ with a range of three octaves.

To prove that his hypothesis was correct, sound waves were conducted, by a mechanical contrivance modelled after the middle ear of mammals, into the water of a vessel containing Mysis, the so-called auditory hairs of which were under observation by the microscope. When notes of a certain group were sounded on a musical instrument, a certain hair would vibrate and disappear from view. Others would also respond, but each to different sets of notes.

Having proved that the different hairs responded to different sound waves, Hensen next determined that Crustacea would react to vibratory stimuli. A resonant bar of wood was floated in a vessel containing free-swimming individuals of the genera Mysis and Palæmon. When the bar was struck, both forms responded by a strong leap away from the source of the sound. Palæmon reacted even more strongly when rendered sensitive by gradual strychnine poisoning.

Milne-Edwards ('**76**), Jourdain ('**80**), Delage ('**87**), and many others have accepted the sense of audition in Crustacea as a fact.

Garbini ('**80**, p. 192) uncritically remarks: "Che i crostacei odano è indubitato; lo sanno anche i pescatori, i quali devono avvicinarsi loro in silenzio" (That crustacea hear is undoubted; this the fishermen know well, who, when they capture them, approach in silence).

Individuals of Palæmonetes varians, which he kept in an aquarium, sprang backward at the slightest sound.

Delage ('**87**) was the first to discover another function than that of audition for the otocyst. By cutting off or destroying the sacs, he proved that they functioned also as organs of orientation. Animals so operated upon (Mysis, Palæmon, and Polybius among Crustacea) were unable to keep their normal upright position in swimming. Blinding intensified the effect, showing that sight aided in orientation.

The otocyst may therefore, in his opinion, be compared to the simplest form of the vertebrate ear, — that found in Myxime, — where the semicircular canals and utriculus serve the purpose of orientation, the sacculus that of audition (to intensity of sound). In the otocyst of Crustacea both functions are performed, he believes, by the same organ.

Verworn ('**91**) proved that the otocyst of Ctenophores served simply for orientation, not being sensitive to sounds.

Bunting ('**93**) confirms the conclusions of Delage as to the function of the otocyst in geotropic orientation. When the otocysts of young crayfish were destroyed, especially if their chelæ were also removed to render their position in the water less stable, there was the same loss of power of orientation that had been observed by Delage.

Kreidl (**'93**), in order to avoid the disturbance to the normal condition caused by the removal of the otocysts, made use of the following ingenious experiment: Palæmonetes newly moulted, and thus without otoliths, were placed in filtered water to which iron filings were added. The otocysts were soon filled with the metallic particles, the chelæ being used to convey them to the opening of the ear in the dorsal wall of the antennule. When now a strong electromagnet was held at one side of, and slightly above the sacs containing the iron otoliths, the shrimp would lean a little to one side, its dorso-ventral axis, normally coincident with the direction of gravity, pointing away from the magnet. This new position of the dorso-ventral axis is proved by mechanics to be the resultant of the two pulls, that of gravity and that of the magnet, the animal accommodating itself to the direction of the resultant of the two forces. If the magnet were held to the right of the animal, the otocysts would be stimulated in precisely the same way as by gravity alone when the shrimp's dorso-ventral axis is artificially turned toward the right; the result is that it attempts to recover its normal position with reference to gravity, and thus turns its vertical axis away from the magnet. Kreidl, going a step further than his predecessors, affirms that the otocysts are not auditory, but exclusively static in function. Thus they should be called *stato*-cysts, not *oto*-cysts.

Still further evidence as to their static function is supplied by Clark (**'96**). The compensation movements of the eyestalks of the fiddler crab (Gelasimus pugilator) and the lady crab (Platyonichus ocellatus) were observed. Tilting a normal animal about its antero-posterior axis gave a parallel compensating movement of the eyes through an angle of 35° to 45°, whether the tilting was to the right or left. On rotation about the dorso-ventral axis, no such movements are shown, though when rotated about the lateral axis, the animal's eyes moved in the opposite direction through an angle of 35°.

If both otocysts were removed, these compensative movements were much reduced, and the general movements of the crab also became very uncertain.

After removal of one otocyst 94 per cent of the animals showed on rotation toward the uninjured side less compensation than uninjured animals. Blinding produced only a slight reduction in the compensatory motions, but when, in addition to this, both otocysts were destroyed, compensatory movements completely disappeared.

Bethe (**'97**), in his physiological work on Carcinas mænas, confirms Clark's results. In a previous paper he (**'95**^{a}) observes that *Mysis can hear after the otocysts have been destroyed*, but with difficulty; also that the animals are more sensitive to low tones than to high.

Thus, until 1898 three views were held as to the function of the otocysts:

(1) That they are purely auditory organs (Hensen and the earlier zoölogists).

(2) That they are both auditory and static in function (Delage and Bethe).

(3) That they are purely static in function, i. e. organs of orientation (Kreidl, Clark, and others).

To determine whether decapod Crustacea really hear, and if so, whether the otocyst is the organ of audition, is the aim of two papers by Beer (**'98, '99**).

In criticising the conclusions reached by Hensen and Bethe, Beer remarks in his first paper that, because decapods were made to react to different sounds, does not prove that these Crustacea responded to *true* sound, or that they heard. These reactions may have been due to their *feeling* vibrations transmitted to the water from the walls of the vessel in which they were confined, — a tactile reaction, or, to use Bethe's term, a "tango-reflex." Experiments with sounds produced in the air Beer considered superfluous, as it is a well-known physical fact that most of the sound waves are reflected from the surface of water.

Beer found that Crustacea reacted strongly to sounds produced in the water by striking partially submerged bells, jars, etc., but only when they were not at a greater distance from the source of sound than that at which vibrations could be detected by *the hand immersed in water.* The animals responded more strongly when near the walls of the vessel; but vibrations could be felt by the hand also in this position more distinctly, even though further removed from the source of the sound.

For animals well supplied with tactile organs, he regards pure sound or pure audition as impossible; because vibrations could be felt as soon as heard, and, this being the case, audition would be useless.

On removal of the otocysts, Palæmon and Palæmonetes still responded to sound waves produced in the water. There was, however, a slight inhibition of the customary reactions, therefore the hairs of the otocyst are probably slightly tactile as well as static in function.

From experiments on many different species of Crustacea, Beer ('98, p. 31) concludes: "Wir haben gute Gründe, dem in Rede stehenden Sinnesorgane der Krebse statische Functionen zuzuschreiben, und haben vorläufig gar keinen Anhaltspunkt, ihm Hörfunctionen, ja den Krebsen überhaupt Gehörsinn, zuzuschreiben."

Hensen's statement that the free auditory hairs of Mysis vibrated to different musical notes is simply an interesting physical fact. Hairs on the back of one's hand will do the same, but they are not auditory. The true sense of hearing is lacking not only in Crustacea, but probably in all other water-inhabiting animals lower than Amphibia, especially in invertebrates.

Beer thus comes back to the opinion of Johannes Müller ('37) expressed sixty years before: That in most invertebrates we find nothing comparable to the ear; and any reaction to sound vibrations should be attributed to a *tactile* rather than to an *auditory sense.*

A few months later Beer ('99) brought out a second paper, describing his experiments with blind shrimps, and answering a criticism of his previous work by Hensen ('99). Here the auditory sense, he urges, ought to be intensified, all possibility of sight entering as a factor into the experiments being effectually eliminated. The conclusions reached by him in his earlier work are verified in this.

General Criticism.

It is a noteworthy fact, that in the experimental work done to determine the function or functions of the otocyst, few of the investigators have acquainted themselves with the finer structure of the organ under consideration; one of the essentials for successful physiological work is a complete knowledge of the anatomical side of the subject. This is well illustrated in Bethe's work on the brain of Carcinas, where anatomical facts, obtained by means of methylen blue, laid the groundwork for his later confirmatory experiments.

Since the dissections by Hensen, little or no morphological work has been done on the otocysts of the Brachyura, yet a deal of physiological work has been attempted.

The experiments of Beer are beautifully worked out, and logical in sequence; yet, while he tried experiments on water-inhabiting animals, no attempt was made to experiment on amphibious decapod Crustacea, such as the fiddler crab. These animals, spending, as they do, a good share of their life on land, would certainly have more need of an auditory organ than decapods which are always beneath the surface of the water.

B. EXPERIMENTS AND OBSERVATIONS.

I. The Otocyst as an Auditory Organ.

That the responses of water-inhabiting animals to atmospheric sounds is nothing more than a myth, has been too well proved by Beer to need further investigation. The well-known physical fact that the larger part of the sound waves are reflected from a liquid surface is enough in itself to confute fables of fishes and crustacea hearing, and coming to be fed at the *sound* of a bell. But since in the case of responses of decapod Crustacea to sound vibrations conducted into the water, the experiments of Beer contradict Hensen's earlier results, repetition of Beer's work, though perhaps not absolutely necessary, may not be out of place.

Methods.

The shrimps to be experimented upon (Palæmonetes) were placed in glass vessels 40 cm. in diameter and 20 cm. deep. Sound waves were conducted to the water by means of a steel pipe one inch in diameter and about two feet long, which was firmly clamped at its upper end and projected into the vessel containing the shrimps; a brass rod was in some cases substituted for the pipe. The pipe and rod were set into vibration either by striking them with a hammer, or by drawing across them, bowlike, a strap of rosined leather. Sounds were also produced by striking glass jars suspended in the water, and by striking the sides of the aquarium itself. The movements made in producing the sounds were completely screened from the view of the shrimps by pieces of cardboard placed over and at one side of the vessel, a small aperture being left for observing their reactions.

Palæmonetes could be made very sensitive to all nervous stimuli by leaving them over-night in sea water containing from 0.1 to 0.2% of sulphate of strychnia. This solution is fatal to a small fish (Fundulus) in five minutes; many of the shrimps die, but the sensory apparatus of those which remain alive is rendered abnormally acute. Blinding was accomplished by simply painting the eyestalks with a thick coat of lampblack and shellac; the otocysts were removed by means of a fine hooked needle, with scarcely any other injury to the animal.

1. *Responses of Palæmonetes to Vibrations transmitted to Water.*

a. Normal Conditions. Under normal conditions, when sound vibrations were transmitted to the water, normal animals responded by a slight leap backwards or to one side, if the source of the sound was within a distance of 20 cm. If an animal happened to be near the side of the vessel, and the sound was produced near the opposite wall 40 cm. distant, the response would be, *not a darting away from the source of the sound*, but a leap back from *the side of the vessel toward the source of the sound.* Again, if an animal was facing the side of the aquarium with its antennæ in close proximity to it, and the opposite wall was sharply tapped with the finger-nail, or lightly with a hammer, the shrimp, as before, sprang away from the side of the vessel *toward the source of the stimulus*. The response was usually well marked, a leap of from 10 to 15 cm. being made.

b. Poisoned with Strychnine. The responses obtained were invariably much stronger and more uniform with animals poisoned by strychnine in the manner stated above, than with normal shrimps. In other respects they were the same, and served merely to emphasize the results obtained by the first experiments. Blinded individuals showed practically the same reactions, but to make sure that the factor of vision was effectually cut out, the eyestalks of the shrimps in the succeeding experiments were all painted.

c. Both Otocysts removed. Of animals from which both otocysts had been removed, all but one gave a more or less strong response to the sounds conducted into the water in which they were swimming. The reactions were not as marked, nor could they be produced at as great a distance from the source of the sound, as in the case of normal animals. Nine individuals were affected by the stimulus when at a distance of about 10 cm.; the rest, only when in still closer proximity. A slight jar imparted to the walls of the aquarium produced essentially the same responses as the transmission of sound to the water by means of the vibrating pipe or rod. Removal of the otocysts has, therefore, only a very slight inhibitory effect upon the responses called forth by sound-wave stimuli in normal or strychnine-sensitized animals.

d. Removal of Antennæ and both Antennules. The removal of the antennæ and antennules, which bear large numbers of delicate *tactile* hairs, very much reduced the reaction of the shrimps to these vibratory stimuli. Only when an animal was in close proximity (5 cm. or less) to the source of the sound, or in contact with the walls of the vessel, would it respond, and then only feebly. Slight jarring of the aquarium produced no reaction, unless some part of the animal's body directly touched the sides or bottom of the jar, or was in contact with the sound-producing instrument.

The above experiments were duplicated on *Crangon vulgaris* with similar, though less marked results, as Crangon is much more sluggish than Palæmonetes.

A third set of experiments was tried with *Virbius zostericola*, a shrimp-like decapod *without otocysts*. Normal animals responded vigorously on striking a glass jar partially submerged beneath the water in which they swam. This response, much increased by strychnine poisoning, was distinctly diminished when both antennæ and antennules were removed.

e. Meaning of these Experiments. All of my experiments confirmed the conclusion of Beer, that free-swimming decapods, whether possessing otocysts or not, will respond to stimuli which are transmitted to them by the liquid medium they inhabit. The next question is, to determine whether this response is caused by the perception of *sound* waves or by the coarser vibrations or jars imparted to the water. In other words, have we to do with true *audition* or with the *sense of touch?*

Beer has clearly shown that there is no such thing as the transmission of pure sound waves from air to water. Coarser waves are imparted to the liquid simultaneously with those of sound, and can readily be felt by the immersed hand.

After making a number of trials with sounds produced as in the preceding experiments, I ascertained that the vibrations not only could be plainly felt by the submerged hand, but also that they could be felt *at a distance from* 10 *to* 20 *cm. greater than that at which the shrimps would react.* This fact does not at all prove that the animals experimented with do not hear, but merely shows that the responses supposedly produced by sound stimuli may be simple tactile reflexes, called forth by vibrations which, since appreciable to the immersed fingers, we may certainly assume to be *felt* by these animals, so well supplied with delicate tactile organs.

That the reaction is really due to tactile stimulus rather than to audition, is indicated by several facts brought out by the experiments:

(1) Animals, when near the wall of the vessel, even though distant from the source of the sound, respond vigorously, *leaping away from the wall and toward the sound.* The wall is set into vibration by the production of the sound, and it is apparently this vibration which affects them, rather than the true sound-waves imparted to the water.

(2) The average distance from the source of the sound at which they will respond is less than that at which vibrations may be felt by the hand.

(3) Removal of the antennæ and antennules which are supplied with numerous *tactile* bristles, inhibits the reaction.

(4) Decapods, such as Virbius, normally without otocysts *respond vigorously;* but removal of antennæ and antennules diminishes their sensibility in a marked degree.

(5) Precisely the same responses as were called forth by the production of sound were also obtained by simply tapping or jarring the walls of the aquarium.

Whether due to tactile stimulus or to audition, the fact remains, that the otocyst has little or no part in producing the reactions observed in the series of experiments; for (1) decapods normally without otocysts respond as vigorously to the same stimuli as those possessing them, and (2) the removal of the sacs from the latter has only a very slight inhibiting effect, which might be due either to the loss of these organs, or to the injury of the nerves supplying the many tactile bristles of the antennule.

Consequently, the otocyst not being the organ by stimulation of which responses to sound vibrations are called forth, and there being no other sensory apparatus in Crustacea especially differentiated for the reception of sound waves, we are led to the conclusion that in decapod Crustacea a true auditory organ is wanting.

The acute tactile sense of decapods may to some extent serve the same purpose that audition does in vertebrates. In mammals the senses of touch and hearing grade into each other. The range of the average auditory organ in mammals is from 30 to 16,000 vibrations per second; waves of less than 30 vibrations per second do not usually produce auditory sensations, but are appreciable to the tactile sense. It is important to note that decapods respond most vigorously to low notes, and not at all to high notes or sounds produced by very rapid vibrations. This fact would seem to be good evidence that the vibrations imparted to the water and perceived by decapods correspond to those which produce tactile rather than auditory sensations in vertebrates.

2. *Responses of Gelasimus pugilator (Brachyuran decapod).*

a. To Vibrations transmitted to Water. On the conduction of sound waves to water by the same means as in the preceding experiments, these fiddler crabs responded, but by no means as vigorously as did the Macrura. They always rested upon the bottom of the aquarium, and reacted by retiring slowly, either from the source of the sound, or from the vibrating walls of the aquarium. In either case the response took place only when the animal was within a few centimetres of the vibrating surface, and was most marked when the antennæ and antennules were in close proximity to it. After blinding the animals and removing their otocysts, no apparent difference could be detected in the reactions called forth, as compared with those of normal crabs; removal of the first two pairs of appendages caused, on the contrary, the responses to almost completely disappear.

b. To Atmospheric Sounds. As the fiddler crab is on land a large part of the time, a number of experiments were tried to determine the effect of aerial vibrations upon them when they were feeding under perfectly normal conditions. A position for observation was selected near a bank which was completely honeycombed by their burrows, where one could see the animals perfectly well, and yet be screened from their view by intervening bushes. If one remained perfectly motionless, the animals would come within a short distance of the observer's place of concealment, feeding as unconcernedly as if no one were near. When a number of crabs were little more than five feet distant, a horn was blown, care being taken to direct it away from them. Although a sound was thus produced loud enough to be heard at some distance, all the animals continued to feed undisturbed.

The striking together of two stones, and the sound produced by striking an iron pipe with a stone (the objects in both cases being held in the hand) also had no effect upon them. On striking the ground with a heavy stone all the crabs within a radius of ten or twelve feet were startled; some of them merely stopped feeding, while others scuttled into their burrows. The same result was brought about by simply stamping upon the ground. If a quick movement was made in the sight of the animals, they at once scattered precipitately to their holes. These observations were repeated a number of times, and on crabs of two different localities, with the same results.

From these experiments and observations, we may draw the conclusion that the fiddler crab, whether in water or on land, does not respond to true sound-stimuli, but is affected only by jars or vibrations transmitted to the water or to the ground. In neither case can they be said to hear. When feeding upon land they do not depend upon an auditory sense to protect them from terrestrial enemies, but rely entirely upon their keen vision and delicate tactile organs.

The statement is generally accepted, that all animals which produce sounds also have a sense of hearing, and this is advanced as an argument in favor of audition in Crustacea. The two well-known examples of sound production among decapods, observed by T. Parker ('78) and Goode ('78), are (1) the stridulation of the rock lobster, Palinurus, where the sound is produced by rubbing the second segment of the antenna against the antennule, and (2) the pistol-like report produced by Alpheus in snapping together the claws of the great chela. As Beer has pointed out, the otocyst is poorly developed in Palinurus; furthermore, no individuals of either species have ever been observed to respond in any way when these snappings or stridulations were produced.

We can no more argue, from these two instances of sound production in decapods, that there is an auditory function in all Crustacea than we can that all fish hear because the drum-fish makes a sound.

The enemies of water-inhabiting crustaceans produce no sounds which would reveal their presence to their prey; the latter would therefore have to rely upon other forms of stimulation for the detection of their foes. Even if it were admitted that they possessed a sense of hearing, yet, as shown both by Beer's experiments and by my own, it must be so restricted in range that they would be able to detect sound produced at no greater distance than that at which the vibrations could be felt by the hand. Such a dull sense as this would be of no practical value in protecting crustaceans from their foes.

Both observation and experiment lead, then, to the following general conclusions:

(1) The reactions formerly attributed to sound stimuli are nothing more than tactile reflexes.

(2) The otocyst has little or no part in calling forth these reactions.

(3) There is no direct evidence to prove that decapod Crustacea hear, and until such evidence has been obtained, we are not warranted in ascribing to the otocyst a true auditory function.

II. The Otocyst as an Organ of Equilibration.

All water-inhabiting, free-swimming animals which maintain a definite position with reference to gravity either during locomotion or when at rest, can thus orient themselves only under one or the other of two conditions:

Either the animal must be normally in a condition of stable equilibrium, keeping its definite position under the influence of gravity like any inanimate body; or, if a position of unstable equilibrium is maintained, the animal must in some way be made sensible of the direction of gravity, and must keep itself in equilibrium by its own efforts.

In the first case merely the mechanical action of gravity is called into play; in the second instance, besides the outside action of a physical agent, a subjective sense of direction and orientation is involved.

In free-swimming decapods the body, moving or at rest, is in a position of unstable equilibrium. The dorsal side being always kept uppermost, the centre of gravity is high up, and a dead individual or an inanimate object of the same size, form, and disposition of weight would at once turn over. These animals must then by some means be rendered sensible to the direction of gravity, in order to be able to maintain a definite position of unstable equilibrium with reference to it. To determine what are the organs which perform the function of equilibration, the following means have been employed in the present investigation:

(1) Removal, or prevention of the action of an organ, and observation of the effects on the equilibration of swimming or walking decapods.

(2) Observation of the effect of such removal on the gimbol-like movements of the eyestalks (compensation movements) when the animal is rotated about its different axes.

(3) Observations on the orientation of animals normally without otocysts.

(4) The effect of the development of the otocyst on the equilibration of the free-swimming larvæ.

(5) The effect on equilibration of the addition of magnetic attraction acting on the otocyst at right angles to the pull of gravity.

In these experiments blinding was accomplished by painting the eyestalks with a mixture of lampblack and shellac. The otocysts were removed under the lens of a dissecting microscope with the aid of a fine needle, bent in the form of a hook. Other parts, such as flagella of antennæ and antennules, were simply cut off with a pair of fine scissors. Palæmonetes vulgaris, being hardy, was the species chiefly employed, but experiments of a like nature were also carried on with Mysis, Crangon, and Gelasimus. A large number of trials were made with each species. When organs were cut off or destroyed, the animals so operated upon were kept under observation for from 15 to 25 days, and the experiments were then repeated, in order to make sure that the effects observed directly after the operation were not due to abnormal conditions produced by nervous shock.

1. *The Removal of Sense Organs and its Effect on Equilibration.*

The normal position in which a shrimp, like Palæmonetes, holds itself while swimming, is very characteristic:

(*a*) The dorsal side of the body is always kept uppermost, its dorso-ventral axis corresponding to the direction of gravity, and its long axis usually lying in a horizontal plane.

(*b*) Shrimps can be overturned only with difficulty, and even if this is accomplished, they right themselves at once.

(*c*) Animals coming to rest upon surfaces not horizontal tend to keep themselves in the horizontal plane, but with the dorsal side always up.

a. Eyes blinded. Nearly fifty animals were operated upon in this way and their movements observed. Placed in an aquarium, they swam about indiscriminately, but always with the dorsal side up, there being little if any rolling from side to side. They were not easily overturned artificially, and when interfered with, righted themselves quickly. The most noticeable difference to be observed between their movements and those of normal animals was the tendency to remain quiet and to hold fast to any object with which they came into contact, thus substituting the sense of touch for that of vision lost. It is apparent, therefore, that some organ or organs other than the eyes play the chief part in equilibration.

b. Both Otocysts removed. Twenty-five animals were operated upon by removing both otocysts. In swimming there was still a strong tendency to keep the dorsal side uppermost, but there was in every case marked rolling from side to side, which occasionally culminated in a complete rotation about the long axis of the body. The animals could be easily overturned, and though they strove to right themselves, it was not accomplished as soon nor as accurately as in normal or blinded shrimps. They were more apt to remain quiet, or to swim along upon the bottom of the aquarium, than to swim free. If the long flagella of the first and second antennæ were removed, rolling motions were increased and also the difficulty in righting themselves if overturned, the flagella being probably used as balancing organs in equilibration; but the extirpation of the otocysts alone brings about a marked loss of orientation, much more pronounced than that produced by simply blinding.

c. Both Eyes blinded and both Otocysts removed. Upon removal of both otocysts and blinding of both eyes, entire loss of the normal position in swimming resulted in twenty-one trials out of the twenty-five made. The animals turn over and over, rotating about the long axis, now in one direction, now in the other; they also pitch forward and backward about their transverse horizontal axis, and often swim upon their backs. They do not resist overturning, unless holding to some stationary object, and make no attempt to right themselves when swimming free. The moment they come in contact with a horizontal surface, such as the bottom of an aquarium, they at once take up their normal position, righting themselves quickly, but if the surface they touch be oblique or vertical, and even if they come in contact with the under side of a horizontal surface, they cling to it tenaciously, taking up a position *with reference to the plane of contact*, and not in relation to the direction of gravity, as is the case with normal animals. Thus the phenomena of orientation completely disappear in the majority of cases when both otocysts and eyes are rendered functionless, at least in the free-swimming animal. When the animal comes in contact with solid objects, the sense of touch asserts itself and the phenomena of orientation are again, to a certain degree, made manifest.

d. One Eye blinded, both Otocysts removed. The conditions here are essentially the same as when only the otocysts are extirpated. There is a well-defined rolling motion in swimming, and if overturned artificially, the animal is very slow in regaining the original position.

e. Both Eyes blinded, one Otocyst removed. In such experiments no effect was produced different from that brought about by blinding alone. There was no evidence of a tilting of the dorso-ventral axis toward the injured side, as might be expected, if the functions of the two otocysts were co-ordinated. Nor was there during swimming a rotation toward the side from which the otocyst had been removed. We may therefore conclude that in the phenomena of equilibration each otocyst, as well as each eye, acts independently.

As check experiments, both antennules were removed *distal* to the otocysts. No abnormal conditions were produced in swimming movements, the wounds healed, and these individuals lived in aquaria as long as normal animals. Where the otocysts were extirpated, individuals were kept as long as four weeks, and after this interval, when blinded, they gave the same evidences of loss of orientation as they did immediately after the operation.

These observations, made upon Palæmonetes, were found to hold true also for Crangon, Mysis, and lobster larvæ. Experimentation with the fiddler crab gave like results. If blinded and deprived of otocysts, the crabs rolled both forward and backward when walking or running; this effect was still more apparent when the animals were placed in the water.

2. *Removal of Sense Organs and its Effect on the Compensation Movements of the Eyes.*

The following experiments, carried out on Gelasinus pugilator, confirm the work done by Clark ('96). When a crab is tilted to the right or left, forward or backward, the eyestalks tend to keep their original directions, thus seemingly moving through a certain angle. Such movements, which have been observed also for the head and eyes of many vertebrates and insects, are called compensation movements, and the angle of movement, the angle of compensation.

The angle of compensation in the fiddler crab was measured by means of the apparatus described by Clark ('96), a small table to which the animals could be securely fastened and tilted about their chief horizontal axis. A scale ruled to degrees enabled one to read accurately the angle of compensation, and the angle through which the animal was turned. The long eyestalks of the fiddler crab make it easy to determine the angle of the eye movements.

The angle through which the animals were turned was in all cases 45° first to the right, then to the left, about the chief, or longitudinal axis of the body. In each experiment fifty animals were used, the average being taken as the angle of compensation. These animals were most of them kept twenty days, and the angle then measured again, thus guarding against abnormal conditions.

a. Normal Animals. In normal crabs the eyestalks are so held as to make an angle of about 22° with the vertical. The eye movements are always correlated, and if the animal's body is tilted to the right (45°) the right eye makes a compensating movement of 18° upward, the left eye one of 25° upward; rotated to the left, the conditions are just reversed, the right eye now moving through an angle of 25°. The movement of the eye of the side toward which the animal is rotated is in each case less by about 7° than that of the other eyestalk. This is due to interference of the carapace with the eyestalk, preventing its passage through a greater angle.

b. Both Eyes blinded. Tilting either to right or left had the same general effect as in normal animals, but the right eye described an arc of only 13°, the left eye one of 20°, or *vice versa.* There is thus a marked reduction in the angle of compensation, a decrease of about 5°, as compared with normal animals. This shows clearly the extent to which vision enters into the orientation of these animals.

c. Both Otocysts removed. The angle of compensation is here reduced to 3° and 5°, respectively, for the eyestalks on the side toward and from which the rotation takes place. Even without rotation the positions in which the eyes are held are not definite, as they are in animals which possess otocysts. The stalks often make an angle of 40° or more with the vertical, and their movements are no longer correlated. This, together with the marked decrease in the angle of compensation, as compared with that of blinded animals, makes it evident that in equilibration and orientation the otocyst plays a much more important part than does the organ of vision.

d. Both Eyes blinded and both Otocysts removed. On rotation it was found that the compensatory movements of the eyestalks were practically wanting. Two individuals only out of fifty showed movements of from 3° to 5°. In the greater number of cases no movement could be detected, and in the remainder the angle averaged less than 1°. There was a still greater tendency for the eyestalks to be held in indefinite positions when at rest, and at unequal angles. Fifteen such individuals were kept in an aquarium more than twenty days, and after this lapse of time practically the same results were obtained, showing that the shock of the operation of removing the otocyst had no effect upon the results of the experiments. Furthermore, removal of the antennules distal to the otocysts had absolutely no inhibiting effect upon the movements of the eyestalks.

This series of experiments corroborates, as far as they go, the conclusions of Clark ('96). It is clear from them that the otocyst is the chief organ in equilibration, though sight also plays an important part in the orientation of these animals.

Since the above work was done (July, 1899) a paper has been published by Lyon ('99) on the comparative physiology of compensatory movements. These movements were studied by him in many vertebrate and invertebrate forms; they were found to exist in insects as well as Crustacea. Using the crayfish, he confirms Clark's results to some extent, but finds that on blinding the animals and removing the otocysts a considerable angle of compensation still persists. This, together with the fact that insects, which lack otocysts, show the characteristic movements, he uses as an argument against the otocyst being an organ of equilibration. Lyon also finds that upon rotation about a vertical axis there is a compensation movement of the eyestalks of the normal crayfish through an angle of 10° to 18°; and, further, that when the animal is rotated about its long axis blinding causes a diminution of 10% in the angle of compensation. His results therefore give a much more important place to vision in orientation than do the conclusions of Clark and myself. However, from the combined results of the experiments of Clark, Lyon, and myself, one cannot avoid the conclusion that, in the fiddler crab at least, the otocyst is by far the most important organ in equilibration; next in order comes vision, and then muscular and tactile sense.

3. *Equilibration of Animals normally without Otocysts.*

Virbius zostericola, a shrimp quite common at Wood's Hole, Mass., does not possess otocysts. Observation and experiment brought out several interesting facts concerning it. In the first place, it is not a free-swimming form. Its normal habitat is on the eel grass, to which it clings in positions indifferent to the direction of gravity. When forced to swim, it does so in a very uncertain manner, with the dorsal side usually uppermost, though this is a position of unstable equilibrium. If overturned artificially (and this is easily accomplished), it rights itself slowly and will cling to the first object it may chance to touch. Removed from its supporting blades of eel-grass, its unstable manner of swimming closely resembles that of shrimps in which the otocysts have been destroyed. If the eyestalks are painted with lampblack, and the animals so treated are placed in a large aquarium, and forced to swim, apparently all sense of direction and means of orientation are lost.

4. *The Effect of the Development of the Otocyst on the Equilibration of Lobster Larvæ.*

As has been shown in the morphological part of this paper, there is no otocyst in the newly hatched larva of either Palæmonetes, the lobster, or the crab, nor is there a functional organ during the first three larval stages. It begins to invaginate only in the second larval stage, and it is merely a shallow cup-like depression in the third stage; not until the next moult do the sensory hairs and otoliths appear.

When we examine the conditions as to equilibration and manner of swimming in the different larval stages, we find that in the first larva the body is not definitely oriented while swimming. Newly hatched lobsters are very unstable in their movements, often swim or come to rest upon their backs or sides, and show a tendency to roll from side to side while swimming. The animal swims by means of the exopods of the thoracic appendages; the abdominal segments are flexed ventrally, and the thoracic endopods, hanging down, steady the rolling motions somewhat. In the second stage the conditions are essentially the same.

In the third stage the larvæ are more stable, though the otocyst is still functionless. This greater stability is explained when the swimming position of the body and appendages is observed (Fig. *B*). The thoracic appendages are now relatively large, as compared with the size of the body. They are allowed to hang down ventrally, and in conjunction with the curved condition of the abdominal segments, serve to lower the position of the centre of gravity in the whole animal, thus rendering its swimming position much more stable.

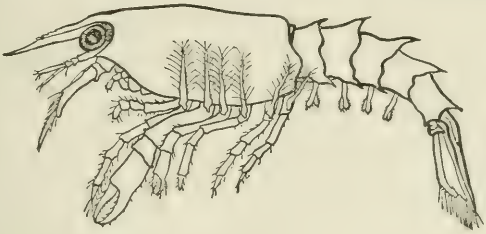

FIGURE *B*.

Lateral view of lobster larva of the third stage, showing swimming position. Magnified 6 diameters.

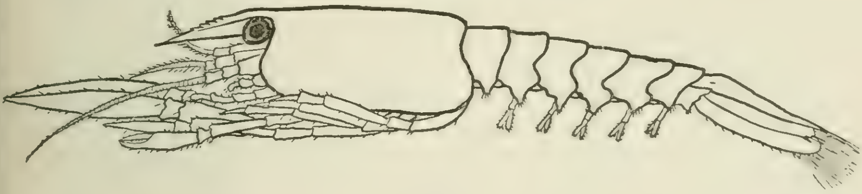

FIGURE *C*.

Lateral view of lobster larva of fourth stage, illustrating the change in swimming position due to the presence of a functional otocyst. Magnified 6 diameters.

Turning now to the fourth larval stage, we find the swimming position of the body entirely changed (Fig. *C*). The abdomen is no longer flexed and curved ventrally, but is held in approximately the same horizontal plane as the cephalothorax, while the thoracic appendages, instead of dragging downward through the water, are held up and forward in a line parallel with the long axis of the body. The great chelæ project in front like the arms of a person preparing to dive, the exopods of the thoracic appendages have been lost, and the larvæ now swim swiftly by means of the abdominal swimmerets.

Although, from the position in which the body and appendages are held, the larva is in unstable equilibrium, it now orients itself very definitely during locomotion, in sharp contrast to the preceding stages. All signs of rolling from side to side, or pitching forwards, are completely lost. The larva swim straight ahead with the body held usually in a horizontal plane and dorsal side up. The same position is also invariably maintained when the animals come to rest.

Thus this sudden change as to form and swimming position in the fourth larva, unfavorable though it is for equilibration, is yet accompanied by more delicate powers of orientation, and greater stability in swimming than are met with in the three earlier stages, where the centre of gravity of the animal is lower. Bearing in mind the fact that the otocyst first becomes functional in the fourth larval stage, we can only conclude that an intimate connection exists between its appearance as an active organ, and the delicate static sense which is suddenly exhibited by the larvæ.

If larvæ of the first, second, and third stages are blinded, their powers of orientation are almost entirely lost, but the same experiment has little or no effect upon the equilibration of the fourth larva. The first three stages thus depend mainly on vision for their imperfect orientation ; in the next stage this function has been largely transferred to the otocyst.

A similar correlation between the development of the otocyst and the appearance of a static sense is found in the metamorphosis of the crab. The pelagic unstable Zoea larva is without otocysts, while the Megalops larva, which exhibits perfect powers of equilibration, possesses these organs well developed, and even containing otoliths, which are absent in the sac of the adult.

The correlation which evidently exists between the formation of the functional otocyst and the sudden increase in static powers exhibited by lobster larvæ is particularly well shown in the marked alteration in the swimming position maintained by the fourth larva, as compared with that of the three earlier stages. Previous to the fourth stage, the lack of a delicate static organ is compensated for by the maintenance of an attitude in swimming which increases the stability of the moving body. Just as Bethe ('95) found that Mysis, deprived of its otocysts, would after an interval of some days recover its power of orientation by curving the abdomen upward and thus, by lowering the centre of gravity, put the body in natural equilibrium, so in the case of the first three lobster larvæ, the attitude maintained is an adaptation for the greater stability of the free-swimming animal, as yet without static organs. But when, in the next stage, the otocyst becomes functional, such an adaptation is no longer necessary, and the sudden change to the unstable swimming position of the fourth larval stage results (Fig. *C*). This is the more natural attitude, and is advantageous to the animal in that it allows of greater speed in swimming.

5. *The Function of the Otoliths.*

At the time when the otocyst was regarded as an auditory organ, the otoliths were supposed to act simply as intensifiers of the sound vibrations, but viewing the sac as a static organ, the rôle played by the otoliths must assume a different aspect. The fact that they are wanting in the Brachyura, which nevertheless exhibit strong powers of orientation, might be used as an argument against their playing any important part in equilibration. But as they are present in the larval crab, and as they disappear only when the otocyst becomes highly differentiated, and when sensory hairs much more delicately constructed than the otolith bristles are developed, this argument loses most of its weight.

For determining the functions of the otoliths two methods may be employed: (*a*) Observing the effect on equilibration and orientation following the removal of the otoliths, or the prevention of the normal process of taking them in after ecdysis. (*b*) Substitution of iron dust or iron filings for the otoliths, and the employment of an electro-magnet to modify the action of gravity. If the otoliths are static in function, the animals should orient themselves with reference to the resultant of the attraction of the magnet, and the pull of gravity.

The first of these methods was attempted by Kreidl (**'94**), but failed, as he was unable completely to remove the otoliths. His results with the second method of experimentation were definite and affirmative. Lyon (**'99**) attempted to repeat and verify Kreidl's work, but his experiments were incomplete and negative in their results.

Otoliths, always normally present in macruran decapods, are lacking for only a short time after ecdysis. So short indeed is this interval, that it is extremely difficult to find otocysts of newly moulted animals which are without otoliths. Nor is it usually possible to prevent a crustacean which has been observed to cast its test, from getting new otoliths into the sac; at least not for a sufficiently long period to allow the animal otherwise to regain its normal condition. Even if placed at once in filtered water, some otoliths soon make their appearance, probably originating from the excreta of the animals themselves.

In lobsters the larvæ regain their normal condition within a much shorter interval after ecdysis than do adult individuals; their digestive tract is also much less likely to contain material suitable for the formation of otoliths. Therefore, after trying in vain to completely remove the otoliths from the sacs of Crangon and Palæmonetes, my attention was directed to lobster larvæ as much more favorable material than the adult shrimps. As they moult at intervals of a few days, it is also much easier to obtain them directly after ecdysis or in the very act itself. So obtained, and placed at once into filtered sea water, larvæ of the fourth stage may be kept without otoliths for from twenty-four to forty-eight hours, and a favorable opportunity is thus given for observing the effect produced by the lack of otoliths on the equilibrium of the animals.

Observations were made on eighteen larvæ of the fourth and fifth stages, all of them being kept free from otoliths for at least twelve hours. Within two hours after moulting most of them swam about actively, and ate greedily when fed with bits of crab's liver. In swimming, however, they show distinctly the phenomena manifested by shrimps which have been deprived of their otocysts. There is both "rolling" from side to side, and "pitching" forward and backward; often they swim with the ventral side uppermost. Much more easily overturned than normal larvæ, they do not right themselves at once, but if turned upon the back, will continue to swim in that abnormal position. If blinded, the loss of equilibrium is still more marked. All these conditions are in strong contrast to the actions of the normal free-swimming larvæ of these stages, which conduct themselves in the characteristic manner already described for Palæmonetes.

The observations having been made and recorded, the animals were killed, and the otocysts dissected out and examined under the microscope. Scarcely a particle of inorganic matter was found in the sacs of sixteen larvæ. In two individuals a few small grains of sand were found in one otocyst, but the other was entirely destitute of otoliths.

From the number of cases observed it seems safe to conclude that the otoliths do play an important part in equilibration, and that it is the pull of gravity upon them which stimulates the sensory hairs of the sac. If the loss of the power of accurate orientation were to be attributed to the abnormal conditions resultant upon ecdysis, it might be said in reply that the larvæ were perfectly normal when observed, as far as feeding and active swimming were concerned, and furthermore that the loss of equilibration disappeared at once when a larva without otoliths was allowed to obtain them. The results of these observations are also confirmed by the following experiments.

The otoliths were removed from the sacs of Palæmonetes by lifting the lid which covers the aperture, and forcing a fine jet of water into the cavity. Most of the sand having been thus washed out, the animals were placed in an aquarium upon the floor of which iron filings had been scattered and were allowed to remain until the iron particles had been taken into the sac in place of grains of sand. As an electromagnet, a steel bar 8 inches long and one quarter of an inch square was used. This was ground down nearly to a point at one end; about the other end were wound many layers of fine copper wire, the termini being connected with the circuit of a small six-celled battery. The shrimps employed in the experiments (Palæmonetes) were blinded by the usual method, — painting the eyestalks with a mixture of lampblack and shellac. The pointed end of the magnet was held about 3 cm. from the otocysts, at one side of and a little ventral to them. Animals with normal otoliths, if blinded, do not respond at all, and are apparently unaffected by the proximity of the magnet; they keep their normal position, dorsal side up, with the sagittal plane of the body coincident with the direction of gravity. If not blinded, they simply move slowly away from the magnet when it approaches too near. When, however, the magnet is brought into close proximity to otocysts containing iron filings, the dorsal side of the animal is turned, not toward the magnet, as might be expected if the changed position were due directly to the action of the magnet on the iron filings, but away from it. If the magnet was changed to a position on the other side of the shrimp, the turning was in the opposite direction, still away from the source of attraction.

The above reaction was distinctly noted a number of times for each of the six animals experimented upon. As Kreidl's work was fairly complete, only one series of experiments was tried in confirmation of his results. When the observations had been completed, the antennules of the six shrimps were removed and the otocysts examined under the microscope. In each case particles of iron were found nearly filling the sac, and if a magnet was held close to one of the latter, the whole antennule was lifted by the attractive force, showing clearly that there must have been an effective magnetic pull upon the otoliths of the live animals during the experiments. I believe there is only one explanation for this turning of the body away from the attracting force, and that is a very simple one. Under normal conditions the body of the shrimp is oriented with reference to gravity, and its dorso-ventral axis approximately corresponds to the direction of this force. If the shrimp rotates around its chief axis either to right or left, say 90°, the direction of the pull of gravity on the otoliths is at once changed, and through the medium of the latter other sensory hairs of the sac are stimulated. As a result, the shrimp turns back in a direction opposite to that in which it was rotated, until it is again in a normal relation to the direction of gravity. The employment of the magnet has no other effect than merely to change the direction of the orienting force. This is now no longer that of gravity alone, but *the resultant* of the two component forces, gravity and the pull of the magnet. The animal now maintains its swimming position in reference to this new line of attraction, its dorso-ventral axis coincident with that line, and as a result the dorsal side is turned away from the magnet. To put it in another way, when the magnet is held close to the right side of the otocyst, the animal is stimulated precisely as it would be if rotated to the right 45°, and it responds as it would normally in righting itself, i. e., by turning its body in the opposite direction through an angle sufficient to make its dorso-ventral axis coincide with the direction of the attractive force; in this case through an angle of 45°.

This single series of observations completely confirm, as far as they go, the very important conclusions of Kreidl. The otoliths are found to play an important part in the functional activities of the otocyst, and the latter is conclusively proved to be a static organ, acted upon by the force of gravity; this force makes itself felt chiefly through the medium of the otoliths, and if they are absent, as described in a preceding set of experiments on lobster larvæ, the function of the otocyst in Macrura is seriously impaired.

6. *The Function of the Hairs of the Otocyst.*

The function of the otocyst hairs of macruran decapods which are in contact with otoliths has been already briefly discussed in the first part of this paper. The stimulus imparted to the hair shaft through the medium of the otoliths makes itself most strongly felt at the labile base of the hair, owing to the rigidity of the shaft and the delicacy of the attaching membrane. At this point, too, the nerve fibre invariably ends, and the stimulus is thus transmitted to it, and at once carried to the brain. In the case of adult Brachyura, however, there are no otoliths in contact with the hairs of the otocyst, consequently the effect of gravity, if not entirely null, must be at least greatly lessened, unless indeed the hairs are so differentiated as to be themselves stimulated by it.

Bethe ('97), acting on the idea that in tilting the animal the difference in the pressure of the water might affect the hairs of the otocysts, placed crabs under very high pressures where the slight difference brought about by tilting would be practically eliminated. But he found that all the phenomena of equilibration still persisted.

It is probable that in the otocyst of Carcinus the thread hairs are the most important sensory organs of the sac. The hook hairs, originally in the larva attached to otoliths, later, with the loss of the sand granules, lose much of their functional activity; the third group of hairs cannot be of great importance, as I could not demonstrate satisfactorily their nerve connections, and their structure alone is such as to preclude their being affected by very delicate stimuli. The thread hairs, however, in both structure and position are fitted for the fulfillment of such a function as has been ascribed to them. The shaft is long, attenuate, only slightly fringed at the tip, and attached at the base by a very thin membrane, which allows free movement to the rigid shaft about this region as upon a joint. I have observed in studying freshly dissected otocysts that a slight tilting of the watch glass in which they were contained caused these hairs to sway extensively.

From Clark's experiments and my own, it was apparent that upon rotation in a horizontal plane, there was little or no compensatory movement of the eyestalks, and that when there is such a reaction, the angle of compensation is not maintained, but the eyes return at once to their original positions. Also, on rotation about the animal's lateral axis, the angle of compensation is not as great, when the rotation is rapid and jerky, as when performed slowly and smoothly. These two facts preclude the possibility of the hairs being affected by movements of the fluid surrounding them, at least to any great extent. For if they were so affected, the angle of compensation should be the same, in whatever plane the animals are rotated, and the position of the eyestalks should be in every case maintained by compensation movements.

There still remain two ways in which the hairs may be so affected as to bring about nervous stimulus. Either they may be lighter than the surrounding fluid, and consequently tend always to float erect, no matter what position the otocyst may take relative to them; or they may be heavier than the liquid contents of the otocyst, in which case they would be affected by gravity directly, and exposed to a greater or less pull according to their different positions in the sac. My observations made on dissections of fresh material of both young and adult crabs, do not confirm the first of these hypotheses. The hairs rarely, if ever, float upright in the fluid of the otocyst; on the contrary they usually project out horizontally, with their tips a little lower than their bases; and such conditions would favor the second supposition, that they are heavier than the surrounding fluid. Unfortunately, when fresh material was at hand, my attention was directed toward other problems, and no dissections or observations were made with the settlement of this question primarily in view. It is, however, a point well worth future experimentation, for the function of these hairs is apparently similar to that of the auditory hairs of the vertebrate cristæ acusticæ, and to clearly show how they are stimulated would throw light on an important problem in the physiology of the vertebrate ear.

SUMMARY.

1. The cuticular lining of the otocyst, found in the basal segment of the antennule of all decapod Crustacea, is cast with the test at each moult. It is composed of thin chitin, and is suspended from the dorsal wall of the antennule, which presents an aperture in Macrura, in the larval stages of Brachyura, and also in adult Brachyura directly after ecdysis.

2. In Macrura a single sensory prominence is present, either on the floor or sides of the sac. In Brachyura there are three sensory regions. The sensory hairs are borne upon these cushions, usually in curved rows.

3. The otolith hairs are heavily fringed, often bent or hooked. In Macrura they are attached to the wall of the sac by a thin bulb of chitin; in Brachyura the base of the hair shaft is inserted into a cup-like depression; both methods of attachment allow the hair to sway freely upon its base.

4. The free hairs of the otocyst, found in the lobster and all Brachyura, are extremely long and attenuate; their basal attachment is delicate, and renders them much more sensitive than the otolith hairs.

5. All sensory hairs are formed as double-walled tubes by numerous matrix cells situated beneath the hypodermis, from which they originate. After ecdysis processes from these cells extend into the shaft of the newly formed hair. In preparation for the next moult these processes

are withdrawn, the matrix cells recede from the base of the old hair, and arrange themselves about the nerve fibre for the formation of the new bristle. There is a period between moults, more or less extended, during which no living substance is present in the greater part of the cavity of the hair.

6. The otoliths are grains of sand taken in from the exterior (first, in the case of the lobster, by the fourth larva) and renewed after each moult; they may lie free in the otocyst, or be attached to the sensory hairs. In Brachyura they are found only in the *Megalops* stage.

7. Glands similar in structure to the tegumentary glands are present in the lobster and crayfish beneath the sensory cushions which bear otolith hairs. They secrete a substance for the attachment of the otoliths to the pinnules of the bristles.

8. The innervation of the otocyst hairs and olfactory bristles is distinctly unlike.

(*a*) The otocyst hairs have each a single nerve element, and the terminal fibre ends in the enlarged base of the shaft without branching.

(*b*) Each olfactory bristle is innervated by numerous ganglion cells (100 or more). The peripheral strand of fibres from these cells extends some distance into the cavity of the hair, terminating free and without modification of any kind.

9. The central terminations of all the otocyst fibres are in two closely connected neuropilar masses at the posterior end of the brain, median to those of the second antennæ, and ventral to the optic centres. The nerve sheaths disappear as the fibres enter the "Punktsubstanz," and the fibrillæ soon separate. They cannot be traced to determinate endings, nor are they ever directly connected centrally, with ganglion cells.

10. Each sensory nerve fibre is composed of numerous fibrillæ, embedded in a semi-fluid "perifibrillar" substance, which in turn is surrounded by a delicate sheath. The flowing together of the perifibrillar matrix causes the beaded or varicose appearances characteristic of methylen blue, and silver impregnations. The fibrillar structure can be demonstrated in both the central and peripheral portions of the fibres.

11. The sensory ganglion cells are all typically bipolar and elongate in form. They are placed at some distance from the base of the hair which they supply, and show no fibrillar structure.

12. In the shrimp-like decapods, such as Palæmonetes and Crangon, a nucleated myelin sheath surrounds each sensory fibre and ganglion

cell, extending from the neuropil of the brain nearly to the peripheral ending of the fibre.

13. Each sensory ganglion cell with its central and peripheral fibres constitutes a single nervous element or neuron. The neurons are trophic units, and direct connection between two neurons was not demonstrated.

14. In those decapods which pass through free-swimming larval stages, the otocyst develops as an invagination of the dorsal ectoderm of the basal segment of the antennule, and becomes functional only at the fourth moult after hatching.

15. Invagination begins at the second larval stage, but the matrix cells which are to form the sensory hairs of the sac, make their appearance in the first larva, being derived from the cells of the hypodermis.

16. During the third stage the sensory hairs are formed below the floor of the shallow sac; at the next moult these become functional, the sac enlarges, and otoliths make their appearance. The otocyst is now functional, the hairs are innervated as in the adult, and more than 100 of them may be present. After the fourth stage the chief changes are the increase in the number of otocyst hairs, and the gradual constriction of the orifice of the sac.

17. In Brachyura the Zoea larva is without a functional sac. In the Megalops the otocyst is open, and contains numerous sensory hairs and otoliths. During the next two stages the aperture closes and takes on the adult condition, without otoliths.

18. Structurally, the otocyst of decapods may be compared roughly to the utriculus of such a vertebrate as Myxine; the sac of Palæmonetes to a single isolated ampulla, and its sensory cushion to a crista acustica. The closed otocyst of Brachyura has three sensory regions and is without otoliths. It therefore approaches in general structure the utriculus of the higher vertebrates. Each sensory element of the otocyst is comparable to a single sensory component in the vertebrate crista. In each there is a modified organ for the reception of stimuli, connected basally with the terminal fibre of a sensory neuron.

19. There is no part of the decapod otocyst which is structurally comparable to the middle ear, semi-circular canals, or cochlea of vertebrates.

20. There is no direct evidence to prove that decapod Crustacea react to true sounds produced either in water or in air. The reactions formerly attributed to audition are probably due to tactile reflexes.

21. The otocyst plays little or no part in calling forth these reactions, and does not function as a true auditory organ.

22. Equilibration is made possible by three sets of organs, the otocysts, the eyes, and the tactile bristles.

23. In free-swimming decapods the otocyst is by far the most important of these static organs functionally, vision being secondary to it. Four facts go to prove this:

(*a*) The removal of the otocysts causes a much greater loss of power of orientation, and a greater decrease in the compensatory movements of the eyestalks, than the loss of vision.

(*b*) Decapods and Entomostraca normally without otocysts either swim in unstable equilibrium, or in a position identical to that which an inanimate object of the same form and weight would take under the influence of gravity.

(*c*) Lobster larvæ without functional otocysts are unstable in their swimming movements, but orient themselves with great accuracy at the stage when the sac becomes an active sense organ.

(*d*) If iron filings are substituted for the otoliths, and an electromagnet is employed to modify the effect of the pull and direction of gravity, shrimps orient themselves with reference to the direction of the resultant pull of the two forces, precisely as they do to the attraction of gravity alone.

24. In lobster larvæ of the third and fourth stages there is a direct correlation between the metamorphosis of the otocyst from a functionless to an active organ, and the changes in the swimming position of the animal. When the sac is inactive (third stage), the swimming position of the body and appendages is an adaptation which places the larvæ in comparatively stable equilibrium. As the otocyst becomes functional (fourth stage), this adaptation is no longer necessary, and a much less stable position is maintained, but one more favorable for rapid locomotion.

25. The otoliths in Macrura and larval Brachyura are the means by which the pull of gravity is transmitted to the hairs of the otocyst. On their complete removal there is loss of equilibration and power of orientation; if iron filings are substituted for them, shrimps may be made to respond to the attraction of an electromagnet.

26. In adult Brachyura otoliths are normally lacking. The otolith hairs have become practically functionless, and the thread hairs are modified in such a way as to make them directly responsive to the attraction of gravity without the aid of the otoliths.

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EXPLANATION OF THE PLATES.

All Figures were outlined with an Abbé camera lucida. Tube length was usually 160 mm., with projection distance to the table, 410 mm. The magnifications are given with the descriptions of the several figures. Drawings were made from sections, unless the contrary is stated. The orientation of the figures is given for each plate.

ABBREVIATIONS.

cl. gl.	Gland cell.
cl. gn.	Ganglion cell.
cl. ma.	Matrix cell.
co'nt. crc'oes.	Circumœsophageal connective.
crs. sns.	Sensory crista.
cta.	Cuticula.
cta′.	New cuticula.
dt.	Duct.
fbr′.	Fibrillations.
fbr. ass.	Association nerve fibre.
fbr. c.	Central nerve fibre.
fbr. n.	Nerve fibre.
fbr. pi'ph.	Peripheral nerve fibre.
fg.	Flagellum.
glb.	Globulus.
gn. olf.	Olfactory ganglion.
h'drm.	Hypodermis.
lab. a.	Anterior lip of orifice to otocyst.
lab. p.	Posterior lip of same.
lu.	Lumen of otocyst.
mal.	Hammer.
mb. sph.	Spherical membrane.
n. at.1	Antennular nerve.
n. at.2	Nerve of 2d antenna.
n'bl.	Neuroblasts.
n'lem	Neurilemma.
nl. tu.	Sheath nucleus.
n. opt.	Optic nerve.
n. ot.	Otic nerve.
n'pil. at.1	Neuropil of antennule.
n'pil. at.2	Neuropil of antenna.
n'pil. opt.	Optic neuropil.
n. teg.	Tegumentary nerve.
of.	Orifice.
ot'cy.	Otocyst.
ot'lth.	Otoliths.
pinn.	Pinnules of hairs.
pr'c. pr'pl.	Protoplasmic process.
rm. l.	Lateral branch of antennular nerve.
ro.	Rostrum.
set.′	Group hairs.
set. fil.	Thread hairs.
set. l.	Lateral hairs.
set. m.	Median hairs.
set. olf.	Olfactory hairs.
set. ot.	Otic hairs.
set. p.	Posterior hairs.
set. ta.	Hook hairs.
set. tac.	Tactile hairs.
tb. set.	Hair tube.
tct.	Tectum of otocyst.
tu. myl.	Myelin sheath.

PLATE 1.

All Figures are of *Palæmonetes.* In Figure 1 anterior is up on the plate; in Figures 2, 3, and 4 the dorsal side is up, and the anterior end in Figure 4 is at the left. Lines numbered *2*, *3*, *4*, *5* in Figure 1 indicate the planes of the sections shown in Figures 2, 3, 4, and 5 respectively.

Fig. 1. Dorsal view of the basal segment of both antennules, showing otocysts and the arrangement of the hairs in the sac. × 30.

Fig. 2. Somewhat oblique transverse section, extending from dorsal anterior to ventral posterior, of both antennules and the rostrum, through the posterior ends of the otocysts (compare line *2*, Fig. 1). × 64.

Fig. 3. Transverse section of right antennule through the orifice of the sac, showing tectum and otoliths (compare line *3*, Fig. 1). × 64.

Fig. 4. Parasagittal section through right antennule and brain, showing the course of the otic nerve, with a single nerve element drawn diagrammatically (see line *4*, Fig. 1). × 64.

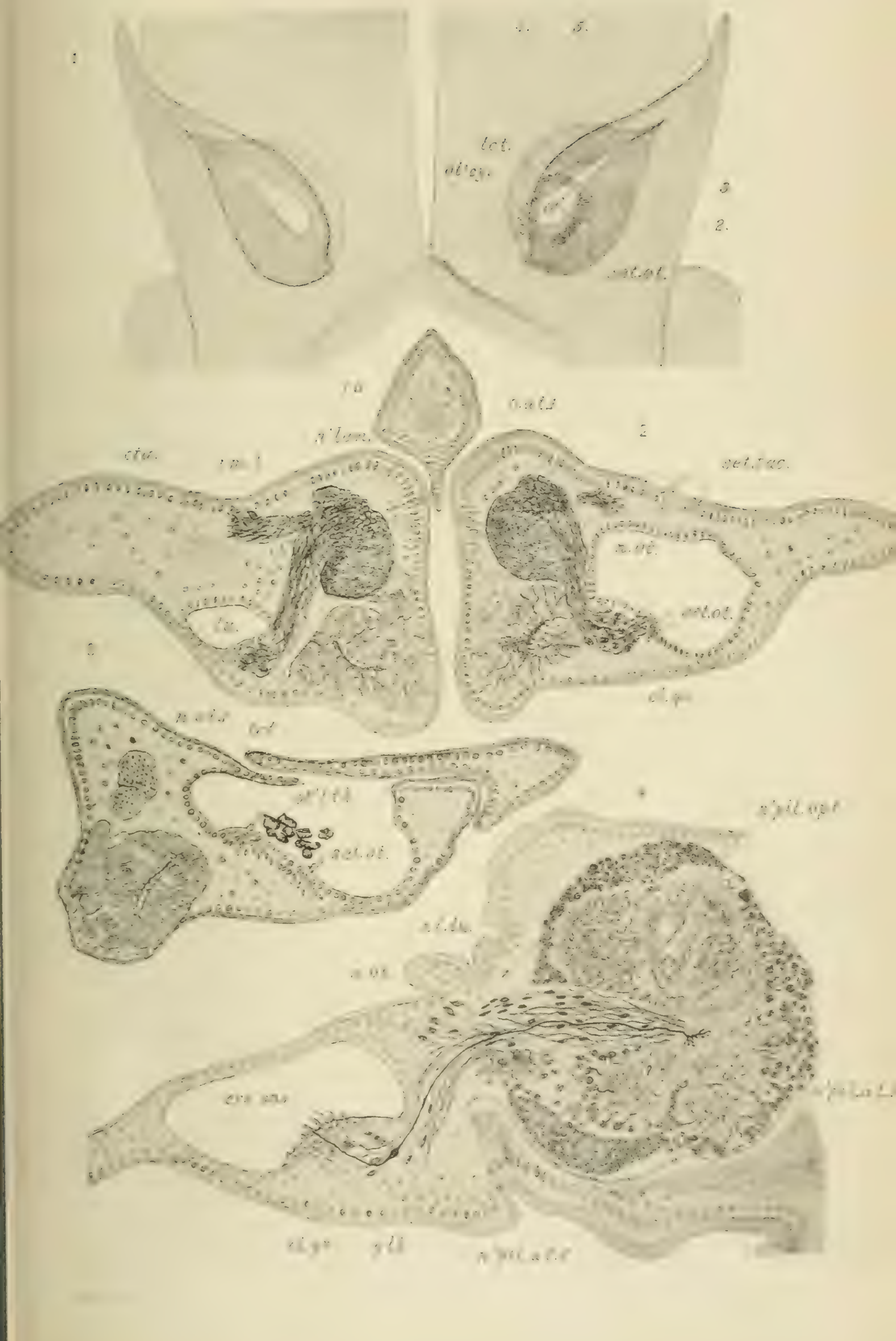
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PLATE 2.

All Figures are of *Palæmonetes.* The dorsal side is up in Figure 5, and the anterior end at the right.

Fig. 5. Parasagittal section through the lateral side of the right otocyst (see line *5*, Fig. 1). × 64.

Fig. 6. Transverse section through the posterior end of the sensory cushion, showing two lateral hairs, the base of a median one and a group of ganglion cells. × 168

Fig. 7. Otocyst hair and matrix cells. × 600.

Fig. 7a. Another otocyst hair and matrix cells. × 600.

Fig. 8. Sensory hair of the otocyst and the ending of its peripheral nerve fibre. × 600.

Fig. 9. Fundament of developing sensory hair from an abdominal exopod, showing matrix cells about the nerve fibre. Methylen-blue preparation. × 600.

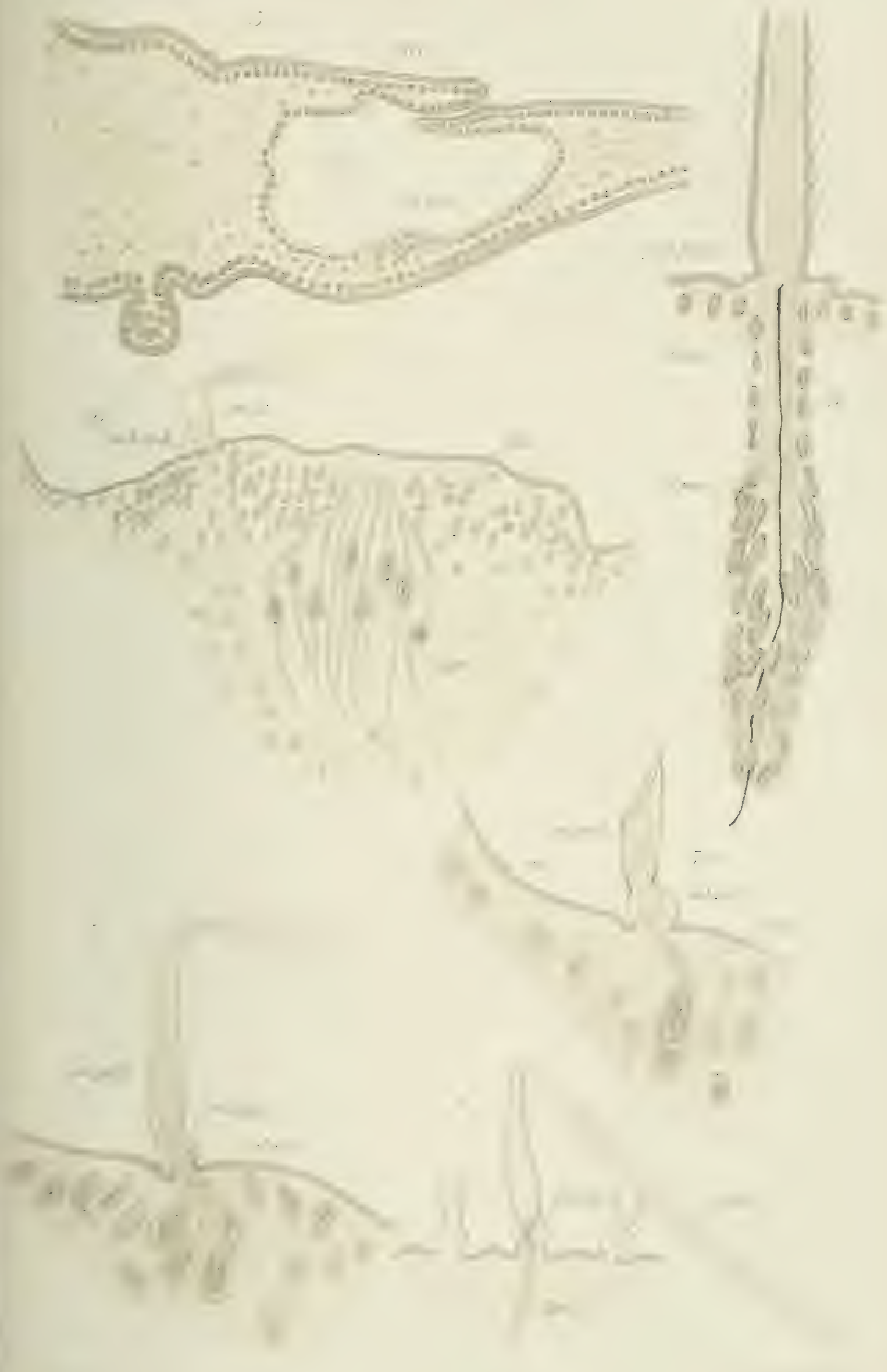

PLATE 3.

All Figures are from methylen-blue preparations of *Palæmonetes*. Anterior is up on plate in Figure 12.

Fig. 10. Part of abdominal exopod showing tubes of developing tactile hairs and their innervation. × 125.

Fig. 11. Peripheral nerve endings in the tactile hairs of the second maxilliped. × 95.

Fig. 12. Dorsal view of antennules and brain, showing sensory neurons and central endings of the otocyst nerve fibres. The peripheral endings in the left otocyst are diagrammatic. × 30.

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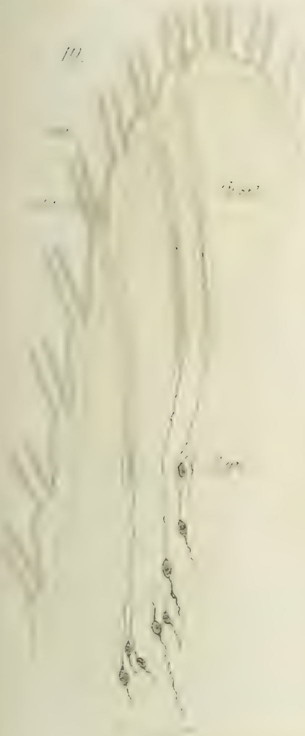

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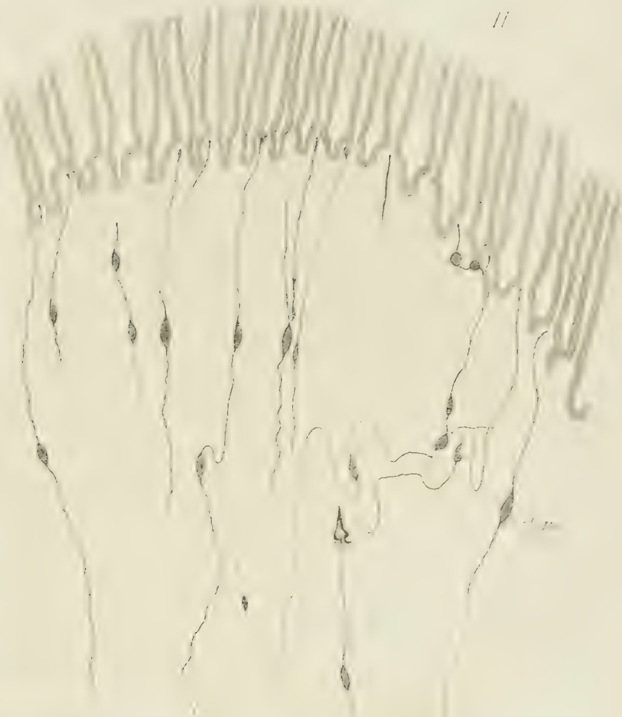

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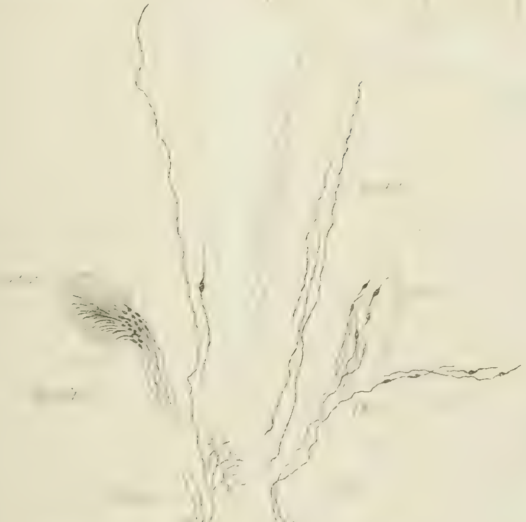

PLATE 4.

Figures 13–18 are of *Palæmonetes*. Figures 19–22 are of *lobster larvæ*. In Figures 19–21 dorsal side is up and the lateral side is at the right; in Figure 22 anterior is at the right, dorsal side up.

Fig. 13. Portion of inner flagellum of first antenna, showing olfactory hairs and their peripheral ganglionic masses. Methylen blue. × 125.

Fig. 14. Gustatory hairs and nerve elements from the basipod of second maxilla. Methylen blue. × 95.

Fig. 15. Fibrillations in peripheral otic nerve fibre. Methylen blue. × 1300.

Fig. 16. Ganglion cell of otocyst and peripheral nerve process surrounded by myelin sheath. × 600.

Fig. 17. Ganglion cell of otocyst, and sheath nucleus. × 1300.

Fig. 18. Ganglion cell of otocyst. Methylen blue. × 770.

Fig. 19. Transverse section through right antennule of first lobster larva. × 168.

Fig. 20. Transverse section through right antennule of second lobster larva; beginning of invagination. × 168.

Fig. 21. Transverse section through right antennule of third lobster larva. × 168.

Fig. 22. Parasagittal section through antennule of second lobster larva. × 168.

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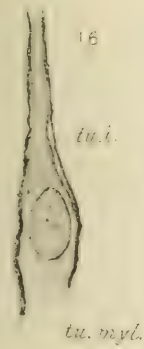

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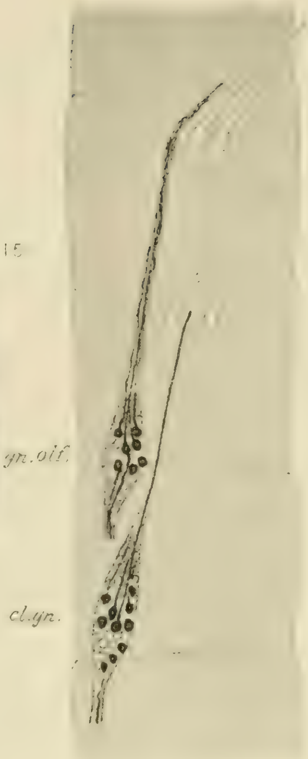

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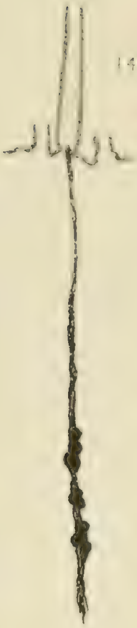

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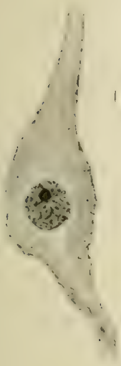

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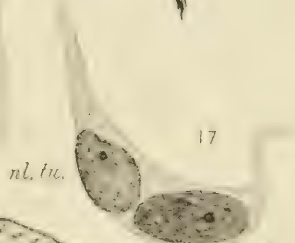

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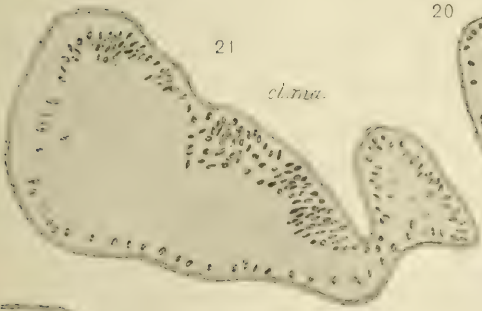

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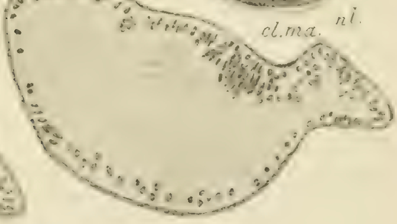

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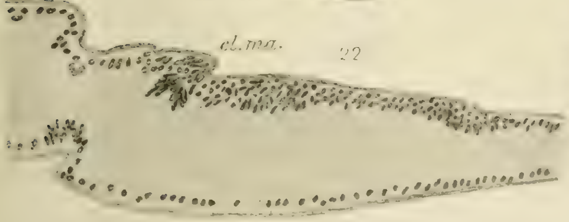

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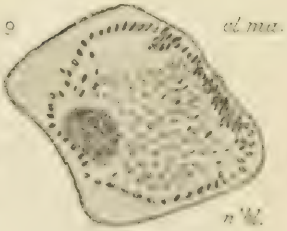

PLATE 5.

All Figures are of *lobster larvæ.* In Figures 23 and 25 dorsal is up, and anterior at the right; in Figure 24 dorsal is up and lateral is at the right; anterior is at the right in Figure 26.

Fig. 23. Parasagittal section through the antennule of the third larva. × 168.

Fig. 24. Transverse section through the posterior part of the right otocyst in fourth larva. × 168.

Fig. 25. Parasagittal section of the same. × 125.

Fig. 26. Diagrammatic dorsal view of floor of right sac dissected out to show arrangement of the hairs and their innervation. Methylen blue. × 168.

Fig. 27. Developing hairs of the otocyst in the third larval stage. × 600.

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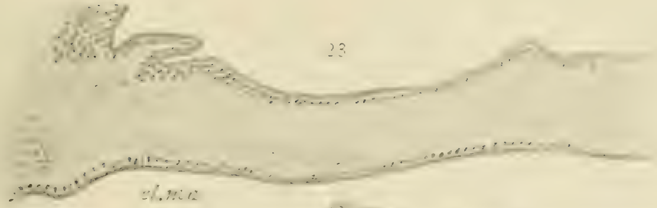

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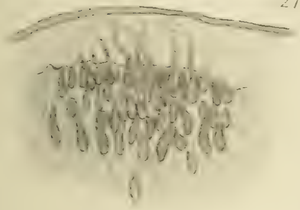

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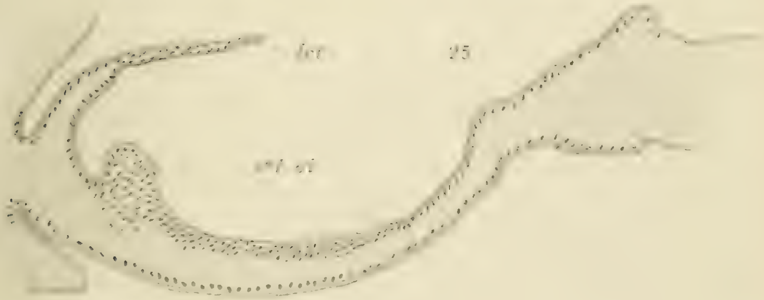

PLATE 6.

Crangon ; in Figure 28 dorsal is up ; in Figure 29 anterior is up.

Fig. 28. Transverse section of both antennules through the sensory cushions of the otocysts. × 95.

Fig. 29. Reconstruction from ten frontal sections through the base of both antennules and the brain. A semi-diagrammatic nerve element is shown at the left in black. × 95.

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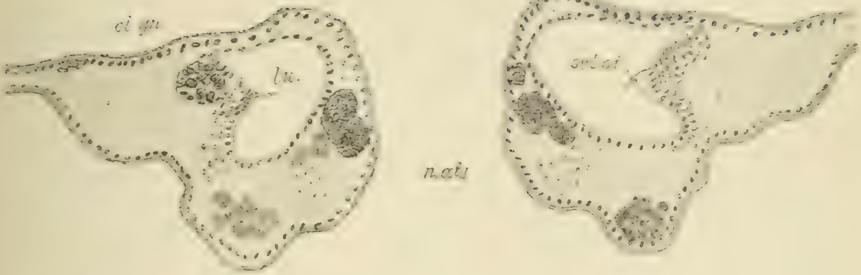
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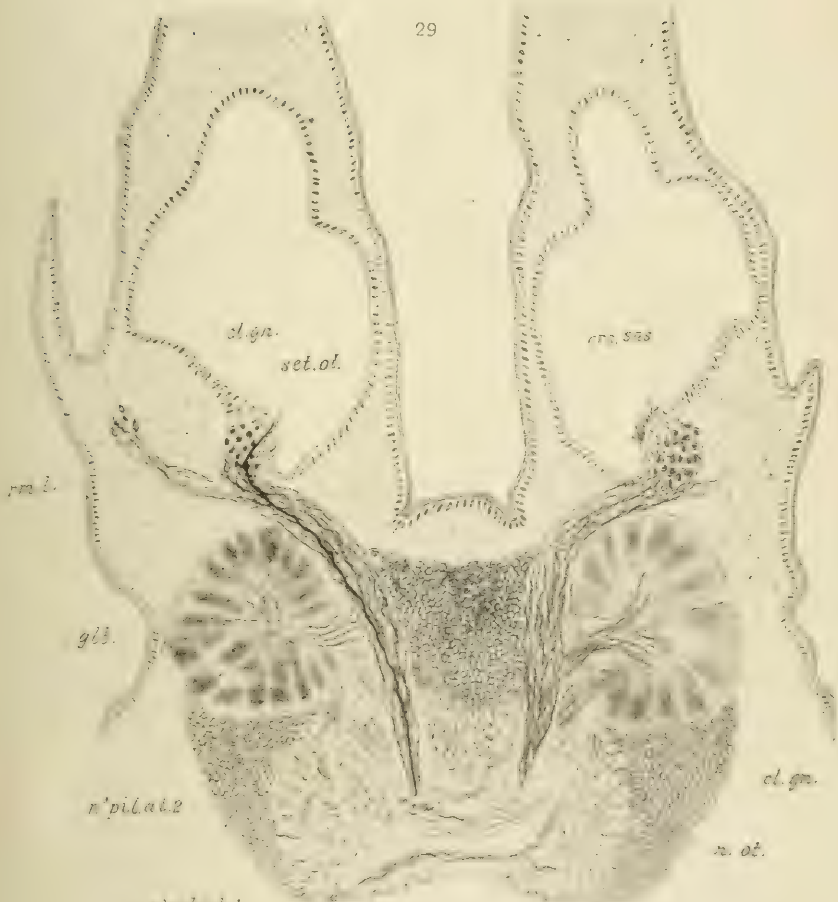
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PLATE 7.

Figures 30 and 31 are of *Crangon.* All others are of *Cambarus.* In Figure 30 dorsal is up and lateral is at the left; in Figure 36 dorsal is up and lateral is at the right.

Fig. 30. Parasagittal section of antennule and brain. × 95.

Fig. 31. Otocyst hair. × 600.

Fig. 32. Olfactory hairs from basipod of second maxilla, showing innervation. Methylen blue. × 95.

Fig. 33. Posterior row of otocyst hairs and their nerve elements. Methylen blue. × 95.

Fig. 34. Tactile hair from scaphognathite of second maxilla, showing innervation. Methylen blue. × 95.

Fig. 35. Transverse section through shaft of otocyst hair. × 770.

Fig. 36. Diagrammatic transverse section of the right antennule through the posterior part of the otocyst. × 15.

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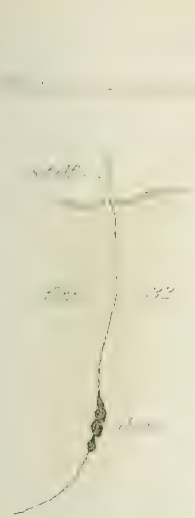

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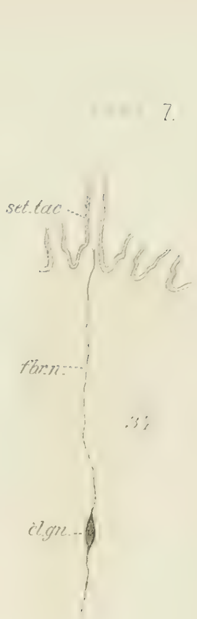
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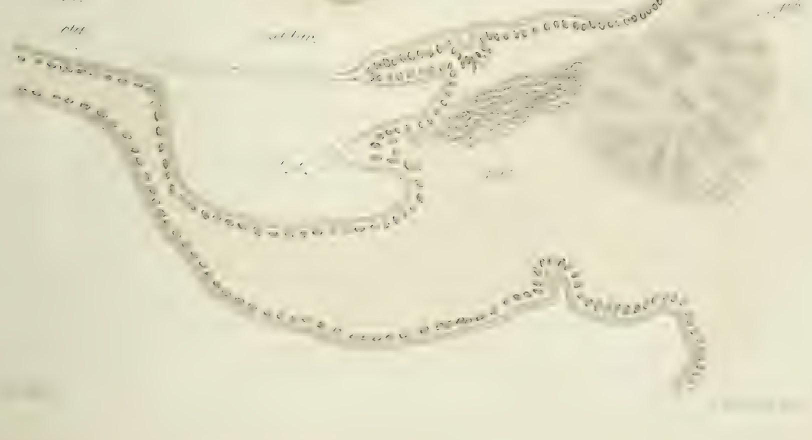


PLATE 8.

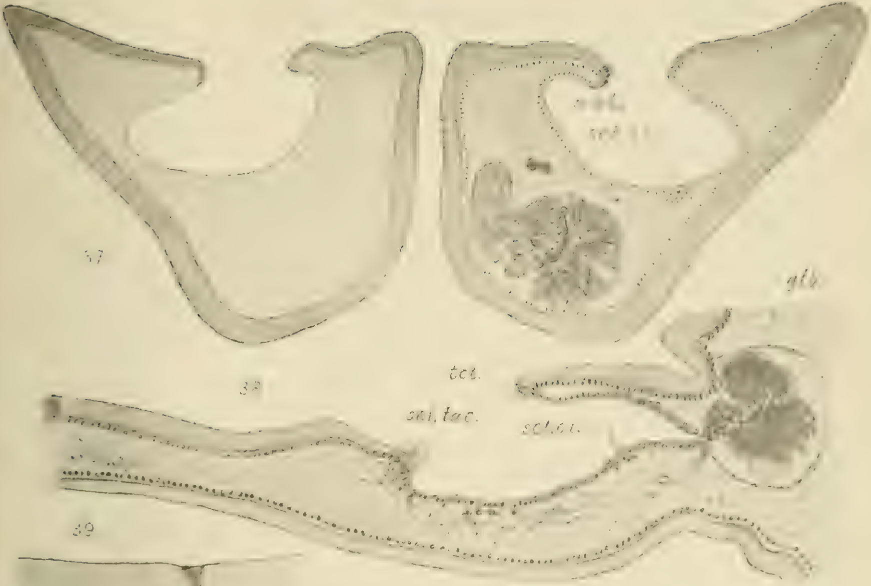
All Figures are of *Cambarus*. Dorsal side is up in Figures 37 and 38; in Figure 38 anterior is at the left; anterior is up in Figure 40.

Fig. 37. Transverse section through the orifice of both otocysts; left antennule is diagrammatic. × 25.

Fig. 38. Parasagittal section through right antennule and brain. × 25.

Fig. 39. Tegumentary gland from the sensory cushion of the otocyst. × 600.

Fig. 40. Dorsal view of the sensory cushion of the left otocyst dissected out, showing the arrangement and innervation of the hairs. Methylen blue. × 62.



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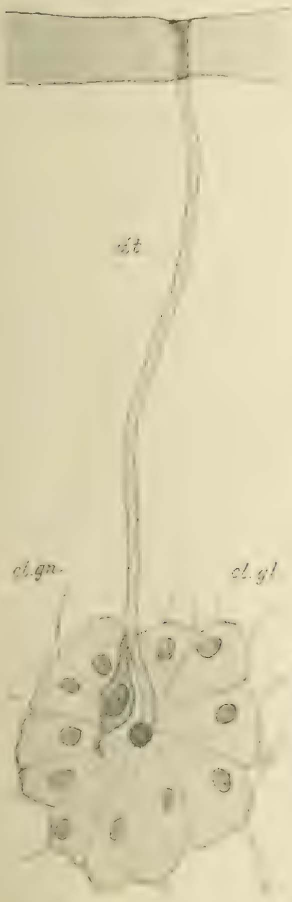

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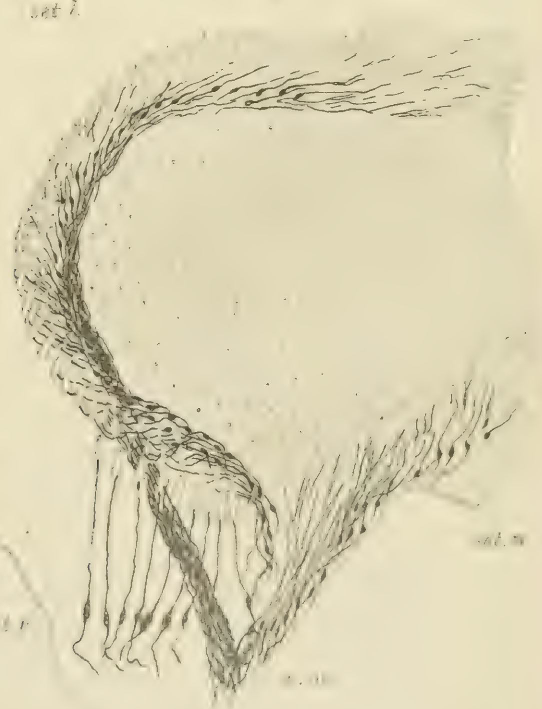

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PLATE 9.

Figure 41 is of *Cambarus*; all others are of *Carcinus*. In Figures 41 and 46 anterior is up; in Figures 42–45 dorsal is up and anterior at the left; in Figures 47 and 48 dorsal is up and lateral is at the right.

Fig. 41. Ventral view of brain, showing central endings of otic and antennular nerves. Methylen blue. × 30.

Figs. 42–45. Outlines of four parasagittal sections through the left otocyst of Carcinas, cut along the lines of section marked with corresponding numbers in Figure 46. Figure 45 is most median, Figure 42 most lateral in position. × 15.

Fig. 46. Dorsal view of both antennules. Numbered lines (*42–48*) indicate planes of section of corresponding Figures. × 8.

Fig. 47. Transverse section through the orifice of right otocyst (see Fig. 46, line *47*). × 15.

Fig. 48. Transverse section through anterior end of the otocyst (see Fig. 46, line *48*). × 15.

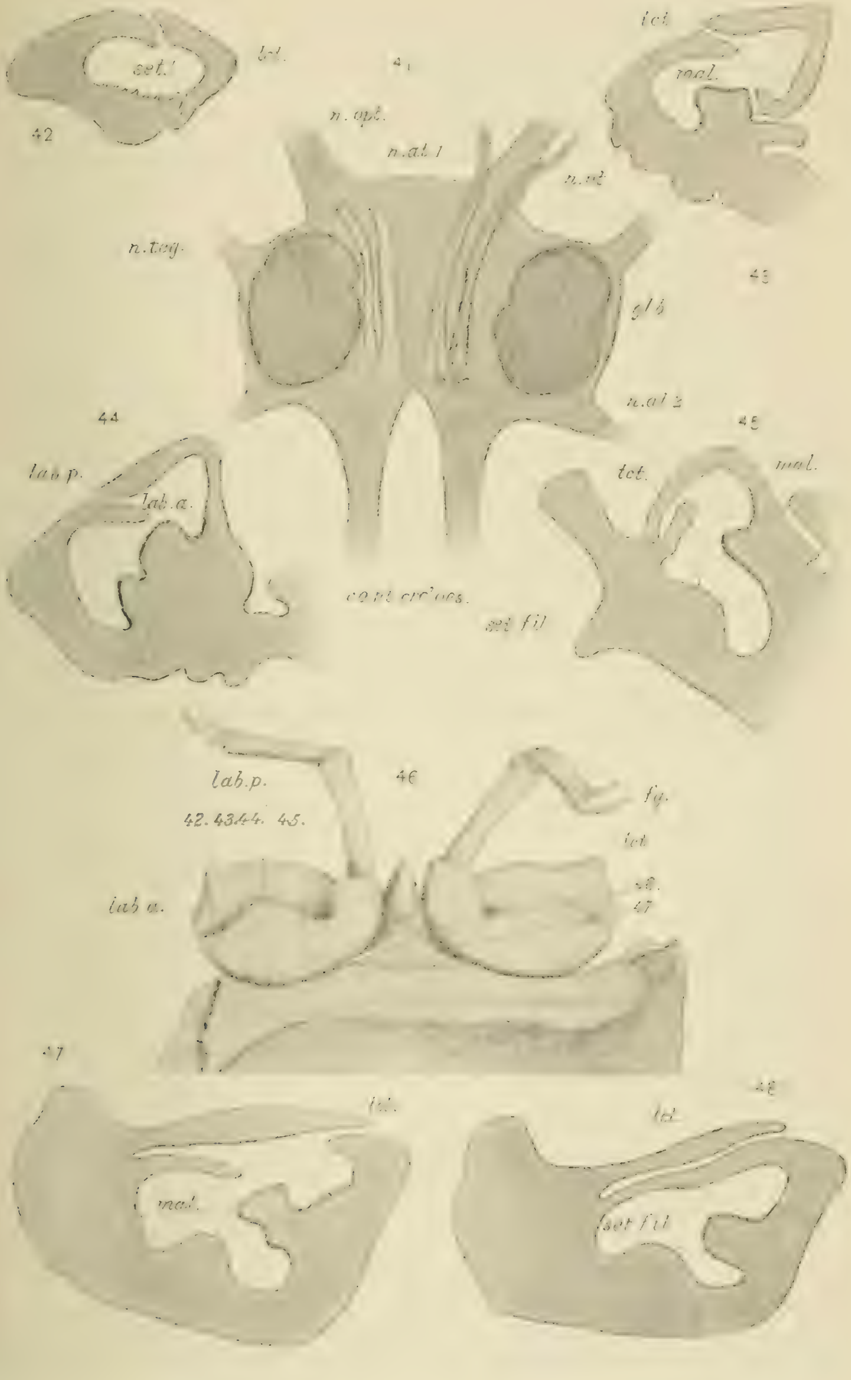
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PLATE 10.

All Figures are of *Carcinus ;* anterior is up in Figure 55.

Fig. 49. Group hair. × 600.

Fig. 50. Transverse section through the sensory cushion of the hook hairs. × 168.

Fig. 51. Hook hair. × 600.

Fig. 52. Portion of outer flagellum of antennule, showing the bases of olfactory hairs and their innervation. × 95.

Fig. 53. Thread hairs and their nerve elements. Methylen blue. × 95.

Fig. 54. Tip of thread hair. × 1300.

Fig. 55. Nearly frontal section, inclining dorsal and forward, through both antennules and brain. × 25.

PLATE 10.

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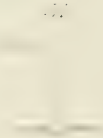

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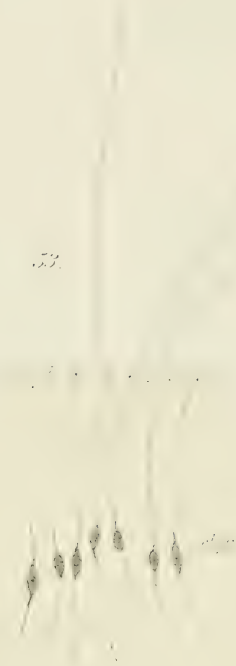

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Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
Vol. XXXVI. No. 8.

ON A COLLECTION OF BIRDS FROM THE LIU KIU ISLANDS.

By Outram Bangs.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
July, 1901.

No. 8. — *On a Collection of Birds from the Liu Kiu Islands.*

By OUTRAM BANGS.

THE Museum has recently acquired from Mr. Alan Owston of Yokohama an interesting collection of birds from the Yayeyama, or southern group of the Liu Kiu Islands. Though consisting of but one hundred and seven specimens, comprising fifty-six species, it contains six forms apparently hitherto undescribed. The collection was made by Mr. Ishida Zensaku and assistants from February to July, 1899, mostly in the Island of Ishigaki; some of the species were taken in the islands of Taketomi, Kobama, Hamarlijima, Kuroshima, Hatojima, and Iruduroto. The systematic sequence adopted is that of Stejneger in his Catalogue of Birds hitherto recorded from the Liu Kiu Islands.[1] I am indebted to the Museum authorities for placing the collection at my disposal for study, and am under special obligation to Dr. Leonhard Stejneger of the United States National Museum. Dr. Stejneger has made extensive studies of the fauna of the Liu Kiu Islands, and his aid and advice in comparing the specimens of the present collection with those in the National Museum have been of great value. I am also indebted to Mr. E. W. Nelson of the Biological Survey for comparing the noddy and sooty terns with those in the Department of Agriculture collection. In the following descriptions all measurements are in millimetres; the wing is measured in its natural curve, and not flattened down on the rule; the tail is measured by thrusting one point of the dividers to the base of the tail feathers and measuring thence to the tip of the longest rectrix. All colors, when definitely expressed, are according to Ridgway.[2]

Sterna melanauchen TEMM.

Two specimens, adult ♂ and adult ♀, from a small island near Taketomi, were taken June 20. [Eggs were collected from June 25 to July 5; a single egg laid on the ground.][3]

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[1] Proc. U. S. Nat. Mus., 1887, Vol. X. pp. 414–415.

[2] Ridgway, R. A Nomenclature of Colors for Naturalists, etc. Boston, 1886.

[3] A list of the Zensaku collection, containing many notes on the distribution, nesting habits, etc., of the species taken, was published by Mr. Alan Owston (Yokohama, 1899). In this paper extracts from Owston's list are in brackets.

Sterna dougalli gracilis (Gould).

Two specimens, an adult ♂ and an adult ♀, taken June 7 on a small island near Ishigaki. [Eggs were collected from June 19 to July 5.] These specimens are extreme of the slender-billed small form to which Gould's name *gracilis* applies. Specimens from western Europe and Africa agree closely in measurements with those from eastern North America and the West Indies. The red bill claimed as a character of *gracilis* may be due to age, many young specimens from America having red bills, while in the adult birds it is black. The differences between the two races of the Roseate Tern in size and in measurements of the bill are well marked.

The Liu Kiu Islands specimens agree in measurements with the Australian form, upon which Gould based his *S. gracilis*, and there can be no doubt of their identity.

The measurements of the two specimens are as follows: —

No.	Sex.	Wing.	Tail.[1]	Tarsus.	Exposed Culmen.
37,304	♂	221	110	20.2	36.6
37,305	♀	216	109	19.4	36.

Sterna fuliginosa crissalis (Baird).

Two specimens from a small island near Iriomote, adult ♂ and adult ♀, taken June 10. [Eggs, one in a clutch, laid on the rock, were taken June 1.]

Sterna bergii boreotis,[2] subsp. nov.

Type. — Mus. Comp. Zoöl., No. 37,301.

A single adult ♂ in full breeding plumage from Ishigaki, June 15, 1899. [Said to breed on Ishigaki.]

Subspecific Characters. — As small as the pale gray *Sterna bergii poliocerca* of Tasmania and South Australia; differing from it in having the wings, tail, and mantle very dark smoke gray, almost mouse gray.

Color. — Type, adult ♂ in full plumage. Forehead, cheeks, lores, ear-coverts, neck all round, and whole under parts, including lining of wing and bend of wing, pure white; crown and long occipital crest glossy black; mantle, wings, rump, upper tail coverts, and upper surface of middle rectrices dark smoke gray, darkest on wings and middle of back, where the color is almost mouse gray; primary quills white; 1st primary with outer web, a band along quill on inner web and tip blackish, with a silvery suffusion which is most marked toward centre of feather; broad outer margin of inner web, below the black tip white; 2nd primary similar but black tip deeper in color and extending a short distance down outer margin of inner web, thus enclosing the white of inner web for a short distance; 3rd, 4th, and 5th primaries like 2nd, but black tip gradually growing deeper in color; outer rectrices above pale smoke gray at tips and along shafts, pale grayish white toward base; 2nd and 3rd rectrices darker on the outer webs and at tip and whitish toward base of inner webs; bill, in dried specimen, dull yellow clouded with olive toward base; feet and tarsi blackish.

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[1] The tails are measured to the end of the second rectrix, the streamer varying too much in length individually to be taken into account.

[2] Boreotis, northern.

Measurements.[1] — Adult ♂, type, wing 344; tail 178; tarsus 28; culmen 62.

Remarks. — *Sterna bergii* was first recorded from this region (breeding on small islands off the north coast of Formosa) by Swinhoe (Ibis, Vol. II. p. 68, 1860); since then two specimens have been noted by Stejneger, both from the Yayeyama Islands, the first in Proc. U. S. Nat. Mus., 1887, Vol. X. p. 392; the second in Vol. XIV. p. 490, 1891. But the question Stejneger raised in 1887, "Will anybody kindly inform me what name properly belongs to the smaller dark birds from the China seas?" has hitherto remained unanswered. My type of *Sterna bergii boreotis* agrees with the descriptions of Stejneger's specimens, and I propose for the small dark northern form of Bergius's tern the trinomial given above. When Saunders wrote his account of Bergius's tern, he had a large series of specimens at his command. He devotes but a few lines to the exceedingly interesting geographical variations of this wide-spread species, and after pointing out, in rather a vague way, how well marked the various races are, ends by including them all under one name.

The principal races of *Sterna bergii* may be indicated as follows: —

1. *Sterna bergii bergii* Licht., South Africa, large, gray of upper parts pale.
2. *S. bergii velox* (Cretzschm), Red and Arabian Seas and Bay of Bengal, large, gray of upper parts very dark.
3. *S. bergii pelecanoides* (King), northern parts of Australia, intermediate between the last two in size and coloration.
4. *S. bergii poliocerca*[1] (Gould), Tasmania and South Australia, small, gray of upper parts pale.
5. *S. bergii boreotis*, subsp. nov., Liu Kiu Islands and Northern China Sea, small, gray of upper parts very dark.

Still another race that may prove distinct is the Polynesian *S. rectirostris* Peale, described from the Fiji Islands.

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[1] Three specimens of *S. bergii poliocerca* in the Mus. Comp. Zoöl. afford the following measurements: —

No.	Sex.	Locality.	Wing.	Tail.	Tarsus.	Culmen.
8,781	♂	Australia.	334	158	31	59.5
12,018	♀ (?)	Melbourne, Aust.	332	173	27	56.
8,782	♂ (?)	Australia.	340	146	30	59.

For further measurements, see Stejneger, Proc. U. S. Nat. Mus., 1887, Vol. X. pp. 393–394.

Anous pullus,[1] sp. nov.

TYPE. — Mus. Comp. Zoöl., No. 37,298.

Two specimens, an adult ♂ and an adult ♀, from a small rocky island near Iriomote, June 10. [Eggs, one in a clutch, laid on the bare rock, were taken July 1.]

Characters. — A large very dark brown noddy with a gray crown, nearest to *A. rousseaui* Hartl. of Madagascar and adjacent islands, from which it differs by being much darker in color and slightly smaller in size.

Color. — Adults, in unworn, full breeding plumage. Narrow superciliary streak, ending above eye, lower eyelid, and a spot on upper eyelid whitish; forehead pearl gray, this color extending over crown and gradually darkening to slate gray on occiput, and thence merging on hind neck into the brown of upper parts; lores and region above the eye below the whitish streak black; upper parts rich dark chocolate brown, with a slight grayish cast; primaries and rectrices dark blackish brown; chin and sides of head blackish slate; rest of under parts deep chocolate brown; lining of wing brownish slate; bill, in dried specimens, black; feet and toes reddish brown.

Measurements: —

No.	Sex.		Wing.	Tail.	Tarsus.	Culmen.
37,297	♂	Topotype.	273	164.5	25.	39.
37,298	♀	Type.	271	159.5	24.5	38.

Remarks. — A comparison of the two specimens upon which I base this new noddy with the material in the National Museum and the Museum of Comparative Zoölogy shows them to be much nearer to *A. rousseaui* than to any of the other forms. The comparison was made with skins of *A. rousseaui* from the Seychelles and Mauritius. The Liu Kiu birds are much darker in color throughout, especially so about chin, sides of neck, and breast, and they are also smaller, the wing of the Mauritius specimen being 285 mm. long, and I have no hesitation in proposing a name for the Liu Kiu noddy.

Compared with other noddies, the differences are still greater; thus the Liu Kiu form is much darker than *A. ridgwayi* Anthony from Socorro and Tres Marias, especially about sides of head and throat, and the crown is darker and grayer.

From *A. galapagensis* Sharpe the new species differs in not having so black a body or such a dark gray crown.

From the noddy of eastern America — true *A. stolidus* — the Liu Kiu bird is very distinct, and can at once be told by its larger size and gray crown and forehead, the forehead and most of the crown in *A. stolidus* being white or yellowish white.

A. pullus differs much from the small slender-billed species, *A. leucocapillus, A. hawaiiensis,* and *A. tenuirostris,* in being larger and having a stouter bill.

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[1] Pullus, dark-colored, dusky.

Puffinus leucomelas Temm.

Two specimens from a small island near Iriomote, taken June 7. [One egg was taken July 1, from a hole in the rock about six feet deep.]

Bulweria bulweri (Jard. & Selb.).

One adult ♀ from Hanarejima, June 25. [Two eggs supposed to belong to this species were taken on the same island, June 20.]

Arenaria interpres (Linn.).

One adult ♂ in full plumage, Ishigaki, May 10.

Charadrius dominicus fulvus (Gmel.).

Two females from Ishigaki, March 1 and June 1.

Aegialitis alexandrina (Linn.).

One specimen, March 13, Ishigaki. [Eggs were collected, April 29 to June 20.]

Ochthodromus mongolus (Pall.).

One ♀ from Ishigaki, June 1.

Actitis hypoleucos (Linn.).

One ♀ from Ishigaki, March 12.

Heteractitis brevipes (Vieill.).

One ♀ in winter plumage, Ishigaki, March 12.

Gallinago gallinago (Linn.).

One ♀ from Ishigaki, March 25.

Limnobænus phæopygus (Stejn.).

Three specimens from Ishigaki, adult ♂ taken May 1, adult ♀ June 20, and a chick June 19. The chick is covered with black down, which on the back is shining blue black, the bill and a patch of bare skin below the eye are yellow.

The wing in the adult ♂ is 105.4, in the adult ♀ 104. Neither of these has white spots on the outer web of 1st primary, such as Stejneger describes. [Nests containing six eggs each were found among reeds from April 10 to July 4.]

Rallina sepiaria (Stejn.).

Two adults from Ishigaki, ♂ taken March 20 (wing 146), ♀ taken April 2 (wing 150).

Gallinula chloropus orientalis (Horsf.).

Two adults, ♂ and ♀, from Ishigaki, taken March 21.

Fuligula fuligula (Linn.).

Two adults from Ishigaki, ♀ taken May 20, ♂ June 13. The male lacks the white spots on the chin.

Anas zonorhyncha Swinh.

Two adults from Ishigaki, ♂ May 10, ♀ June 1. [Many nests were found placed on the ground among grass, and eggs, seven in a clutch, taken from April 19 to June 25.]

Nettion crecca (Linn.).

One female from Ishigaki, March 7.

Dendrocygna[1] javanica (Horsf.).

Two adults from Ishigaki, ♂ taken May 25, ♀ June 1. [Nests were found on the ground among tall grass, and eggs, six in a clutch, taken from May 31 to June 21.]

Sula sula (Linn.).

Two specimens, adult ♂ from Iriomote, June 20, adult ♀ from Ishigaki, June 15. [Eggs were found two in a clutch, on outlying rocks, May 12 to June 13.]

Gorsachius melanolophus (Raffles).

Two adults from Ishigaki, ♂ March 23, ♀ June 7.

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[1] This name is by many ornithologists improperly spelled, "Dendrocycna." Swainson's original spelling was "Dendrocygna."

Demiegretta ringeri Stejn.

One fine adult female, taken in Ishigaki, March 25. This skin agrees with Stejneger's description, and the northern reef heron is a valid form, differing, as pointed out by Stejneger, from the southern reef heron in its gray head and occipital crest. It is, however, not recognized by Sharpe in the Catalogue of Birds in the British Museum.

Nannocnus eurythmus (Swinh.).

Two adults from Ishigaki, ♂ taken March 25, ♀ June 10. [Nests built in reeds about two feet from the ground, containing six eggs each, were found from May 19 to July 3.]

Pyrrherodias manillensis (Meyen).

Six specimens, all from Ishigaki, adult ♂ June 20, adult ♀ May 20, and four nestlings June 1. [Eggs were taken from April 22 to May 19. The nests were placed on oak and other trees, at from 20 to 30 feet from the ground, and usually contained four eggs each.]

This heron was first recorded from the Yayeyama Islands by Stejneger in 1891, who doubtfully referred[1] it to *Ardea purpurea* Linn., but pointed out differences from that species. At that time the relationship of the two members of this genus, *purpurea* and *manillensis*, was not understood. The Ishigaki specimens appear to be typical *P. manillensis*, though I have had but few skins for comparison.

Turnix taigoor (Sykes).

Four specimens from Ishigaki, adult ♂ taken April 25 (wing 77), adult ♀ April 25 (wing 84), and two chicks taken April 12. [Eggs, four in a clutch, were taken from March 17 to July 3.] This is the *Turnix blakistoni* (Swinh.) of Stejneger (Proc. U. S. Nat. Mus., 1886, Vol. IX, p. 635). Dr. Stejneger now agrees with me in the identity of these two forms.

Sphenocercus medioximus,[2] sp. nov.

Type. — Mus. Comp. Zoöl., No. 37,349.

Two adults from Ishigaki, ♂ taken March 9, ♀ March 7. Specimens were secured on this island from February 2 to June 5. [Nests containing two eggs each were found on trees at from six to ten feet from the ground, between April 25 and June 2.]

---

[1] Proc. U. S. Nat. Mus., 1891, Vol. XIV. p. 493.

[2] Medioximus, middlemost, holding a middle place.

Characters. — Nearest in color to *S. permagnus* (Stejn.) from the middle group of the Liu Kiu Islands, but much smaller, being little larger than *S. formosæ* (Swinh.) of Formosa.

Color. — Type, adult ♂. Forehead yellowish oil green, slightly shaded with chestnut toward crown; rest of upper parts dark oil green, the feathers of the cervix, sides of head and neck and upper back, pale gray below the green tips, this color showing through a little, giving a hoary cast to these parts; rump and upper tail coverts a little brighter; primaries slaty black with a perceptible greenish tinge toward ends, the three outer ones narrowly edged with yellowish; secondaries, alula, and middle coverts slaty black somewhat washed with green; middle coverts and secondaries bordered externally with yellow; rest of wing and scapulars oil green with a slight wash of chestnut on shoulder; under parts yellowish oil green; middle of belly and striping on flanks yellowish white; under tail coverts (reaching to end of tail) dark oil green broadly edged with straw yellow; rectrices above olive green, below slaty black with grayish tips; under surface of wing slaty.

Adult ♀, similar to the ♂ but duller in color throughout, and lacking the slight chestnut suffusion on crown and shoulders, and with the grayish tinge of cervix, upper back, and sides of head much less pronounced.

Measurements. — Adult ♂, type, wing 193.5; tail 133; tarsus 26.8; exposed culmen 19. Adult ♀, topotype, wing 192; tail 129; tarsus 26; exposed culmen 18.6.

The Green Pigeon differs in the islands as follows: *S. permagnus* is confined to the middle group of the Liu Kius, while *S. medioximus* is peculiar to the southern group; *S. formosæ* belongs further south still, to the island of Formosa.

Stejneger's type of *S. permagnus* is in the Museum at Tokyo, and I have not seen specimens of the species. In addition to the species here described being intermediate in size between *S. permagnus* and *S. formosæ*, it differs slightly in color from either of the two. In *S. medioximus* two sets of wing coverts are bordered with yellow, and the male has a decided wash of chestnut on both crown and shoulders. Stejneger especially describes his type as having only one set of coverts "the outer great coverts" edged with yellow. If the type of *S. permagnus* be a male, as was supposed, then the chestnut wash on the crown and shoulders of *S. medioximus* is a distinctive character, and yet again very different from the strong coloring of these parts in *S. formosæ*.

Chalcophaps indica (Linn.).

Two specimens, ♂ and ♀ adults, from Ishigaki. The ♂ taken March 20, the ♀ taken June 10. [Many nests were found, containing two eggs each, usually placed in dead trees at from six to ten feet from the ground.]

The two Ishigaki skins differ slightly from two Indian specimens of true *C. indica* with which I compared them. In the Liu Kiu birds the band on the lower back between the two gray bands is not coppery bronze, but is dull black, almost without metallic lustre, and the male has a much greater amount of gray on back and upper neck.

A green-winged dove was described by Swinhoe from Formosa as *C. formosana*, but is not recognized as distinct from *C. indica* by Count Salvadori, in the British Museum Catalogue (Vol. XXI. pp. 514–520).

Megascops elegans (Cassin).

Two adults from Ishigaki, ♂ taken March 25, ♀ March 23. Specimens were taken from March 1 to June 3. [Eggs, two in a clutch, were taken from holes in trees, seven to fifteen feet from the ground, from May 14 to June 27.]

Ninox japonica (Temm. & Schl.).

Three specimens from Ishigaki, adult ♂ taken April 20, adult ♀ April 15, and a half-grown young, no date. These skins agree with Japanese specimens. The wing of the adult ♂ measures 215, of the adult ♀ 210.

Accipiter gularis (Temm. & Schl.).

Three specimens, a ♀ (?) not in full adult plumage taken June 1, an adult ♂ March 25, and a downy nestling June 27, all from Ishigaki.

Butastur indicus (Gmel.).

Two specimens from Ishigaki, neither in full plumage, the ♂ taken June 1, the ♀ March 23.

Halcyon coromanda rufa (Wallace).

Two specimens from Ishigaki, adult ♂ and ♀, both taken April 25. Specimens were secured in Ishigaki and Taketomi from April 5 to June 10. [Eggs, three in a clutch, were collected from June 1 to June 21. The nests were in holes in trees at about ten feet from the ground.] I follow Dr. Stejneger in provisionally referring the Liu Kiu Ruddy Kingfisher to this form.

Anthus maculatus Hodgs.

One female taken in Ishigaki, April 7.

Motacilla lugens Kittl.

One adult ♂ in full spring plumage, taken in Ishigaki, June 1. This seems rather a late date for *M. lugens* to be in the Liu Kiu Islands.

Hypsipetes pryeri Stejn.

Five specimens from Ishigaki, an adult ♂ taken Feb. 29, an adult ♀ April 30, and three recently hatched young April 21. [Skins were also obtained in Kabama, and eggs, four in a clutch, were taken from April 2 to June 25.]

Merula pallida (Gmel.).

Two adults from Ishigaki, ♂ February 20, ♀ May 1. (Many specimens were taken in Ishigaki up to June 20.)

Merula chrysolaus (Temm.).

Two specimens from Ishigaki, adult ♂ May 7, adult ♀ February 18. [Skins were collected in Ishigaki between February 18 and June 7.]

Merula obscura (Gmel.).

Two adults from Ishigaki, ♂ February 22, ♀ March 1. [Obtained in Ishigaki between February 20 and March 1.]

Monticola solitaria (Müll.).

One adult ♀, Ishigaki, March 23.

Terpsiphone illex,[1] sp. nov.

Type. — Mus. Comp. Zoöl. No. 37,363.

Two specimens from Ishigaki, an adult ♂ April 25, and an adult ♀ May 31. [Specimens were taken between April 25 and June 20. Eggs, four in a clutch, between May 12 and June 13.]

Characters. — Nearest to *T. princeps* (Temm.) of China and Japan, but smaller; rectrices narrower and squarer at ends; wing shorter; primaries very short and decidedly narrower and more pointed at ends; *wing formula different* — 4th primary longer than 5th (these two equal in *T. princeps*, or 4th slightly shorter than 5th); feathers of crest in the ♂ all narrower, less rounded; colors much as in *T. princeps*, except less white in axillas and lining of wing; feathers of crest in the ♂ steel blue instead of purplish; sides more heavily washed with brown.

The ♀ differs from the ♀ of *T. princeps* in the same manner as does the ♂, *i. e.*, it is smaller; in having narrower, shorter, more pointed primaries; narrower rectrices; crest feathers narrower and bluer, less purplish in color.

---

[1] Illex, alluring, enticing.

Color.—Adult ♂, head all round, throat, and jugulum blue black, rather more purplish on throat than on crown; back and scapulars glossy prune purple; upper tail coverts and tail blue black; wings black edged with purplish brown; middle of belly and under tail coverts white; sides and flanks heavily washed with dark purplish brown; axillas dull brownish black with white tips; under primary coverts black; under wing coverts white streaked with pale brown.

Female, crown blue black; sides of head and cervix dark gray; throat dark gray becoming paler on jugulum; back chestnut, many of the feathers glossy purplish maroon at ends; tail dark purplish brown; wings hair brown edged with hazel, deeply so on secondaries and tertials; middle of belly and under tail coverts white; sides and flanks washed with purplish brown; lining of wing as in the ♂, except primary coverts are hair brown instead of black.

Measurements. — Adult ♂, type, wing 88; tail, to end of middle rectrices 246.5, to end of longest other rectrices 113; greatest width of outer rectrix, 8.8; tarsus 14.4; exposed culmen 15.4.

Adult ♀, topotype, No. 37,364, wing 82; tail 80; tarsus 14; exposed culmen 15.4; width of outer rectrix 9.2. [In adult males of *T. princeps* the wing ranges from 92 to 94, and the greatest width of the outer rectrix is 11.4. In the adult females the wing measures from 88–90, and the greatest width of the outer rectrix is 12.]

Remarks. — This appears to be the first record of a Paradise Flycatcher from the Liu Kiu Islands. Besides being considerably smaller than a *T. princeps*, it differs noticeably in its short, narrow, pointed primaries and narrow rectrices, and in having the 4th primary longer than the 5th. Like so many of the breeding birds of these islands, it is a well-marked island species.

Zanthopygia owstoni,[1] sp. nov.

TYPE. — Mus. Comp. Zoöl., No. 37,367.

One male from Ishigaki, June 20.

Characters. — Nearest to *Z. narcissina* of Japan, but wing much shorter, due chiefly to the shortening of the primaries; *wing formula different* — 2nd primary shorter than 6th, 3rd about equal to 5th, 4th longest. In *Z. narcissina* the 2nd primary is much longer than 6th, 3rd equals 4th, these two longest and longer than 5th. In color the island bird is very different, the back is dark green, not black, the yellow frontal band extends all the way across base of culmen, the throat and breast are clear gamboge yellow, not orange.

From *Z. zanthopygia* (Hay) the species can be distinguished by its yellow eyebrow (white in *Z. zanthopygia*) and differently marked wing.

Color. — Male, apparently fully adult (♀ unknown), narrow frontal band, extending directly across base of culmen and thence over eye to the supra-auricular region, gamboge yellow; pileum, cheeks, back, and scapulars dusky olive green ; rump bright gamboge yellow ; upper tail coverts and tail black ; wings dark hair brown, the lesser coverts dull, dark plumbeous ; a large white wing patch, formed by the white color of the middle and most of the greater coverts ; one or two (on each side) of the longer tertials narrowly edged with whitish for the basal half of the outer web ; throat, jugulum, and breast bright gamboge yellow, becoming yellowish white on belly and under tail coverts ; sides and flanks washed with olive green ; lining of wing and narrow inner margin of wing feathers, below, white.

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[1] Named in honor of Mr. Alan Owston.

Measurements. — Type ♂, wing 67 ; tail 45 ; tarsus 15.8; exposed culmen 10.2 ; distance from tip of longest secondary to tip of longest primary about 15.

Remarks.—In Proc. U. S. Nat. Mus., 1887, Vol. X, pp. 406-407. Stejneger pointed out the structural differences between the Liu Kiu species and *Z. narcissina* : he, however, had but one young example of the island species, and on this account refrained from giving it a name. The one skin obtained by Zensaku bears out all the structural characters, and besides shows marked color differences from either *Z. narcissina* or *Z. zanthopygia.*

The type of *Z. owstoni*, a male, appears to be in full breeding plumage, and if so, the dark olive green color of the back is unlike any other species, and would alone distinguish the Liu Kiu form.

Cisticola brunniceps (TEMM. & SCHL.).

Two adults from Ishigaki, ♂ taken March 7, ♀ June 1. The fantail warbler is said to be the most abundant bird in the islands. [It builds its nest in grass a foot or two above the ground. Eggs, as many as seven in a clutch, were taken from March 25 to June 30.]

Cettia cantillans (TEMM. & SCHL.).

One adult ♀ from Ishigaki, March 5. [Six specimens were taken on Ishigaki between March 5 and April 7.]

Cettia cantans (TEMM. & SCHL.).

Two specimens from Ishigaki, ♂ taken March 25, ♀ April 6. [Specimens were secured between February 18 and April 6.]

Hirundo rustica gutturalis (SCOP.).

Two adults from Ishigaki, ♂ April 4, ♀ April 3, 1899. [Four birds in all were obtained on the island between April 2 and April 5.]

Pericrocotus tegimae STEJN.

A pair of adults from Ishigaki, the ♀ taken June 20, the ♂ June 10. These specimens agree exactly with Stejneger's type.

Lanius bucephalus Temm. & Schl.

One adult ♀ from Ishigaki, May 10, 1899. I have compared this skin with an extensive series from Japan, and find it identical with mainland birds of the same sex in corresponding plumage.

Parus stejnegeri,[1] sp. nov.

Type. — Mus. Comp. Zoöl., No. 37,392.

Three specimens from Ishigaki, adult ♂ February 27, adult ♀ June 1, and a nestling June 7.

Characters. — Not nearly related to any known species; general coloration gray-blue, black, and white; under tail coverts mostly black; outer rectrices with no white, except a *very narrow* tip on the outer pair; no white patch on nape, a few feathers of this region with partly concealed white spots only noticeable when the feathers are disturbed; general coloration of nestling greenish and dull yellow, showing the probable affinities of this species to some of the yellow and green titmice, such as *P. jerdoni*, *P. inseparatus*, etc., which have black under tail coverts and but little white in the tail.

Color. — Adult ♂ type, a large white auricular patch; rest of head, throat, jugulum, and neck glossy blue-black; a few feathers on middle of hind neck with small semi-concealed white spots; back, rump, and upper tail coverts dark plumbeous, slightly paler on lower rump; scapulars and broad edgings to greater and lesser wing coverts plumbeous; some of the greater coverts tipped with drab-gray, forming a broken and inconspicuous wing bar; rest of wing grayish black, primaries edged with light plumbeous, secondaries with greenish gray, and tertials rather more broadly on outer webs with grayish white; primary coverts greenish gray; a broad black stripe down middle of under parts, from jugulum to under tail coverts; sides and flanks dull olive gray, much paler and more drabby along edges of central black stripe and below the black of jugulum and sides of neck; under tail coverts black, slightly edged and tipped with dark plumbeous, one or two of the shortest lateral ones a little marked with white; rectrices, below blue-black, above, broadly edged on outer webs with dark plumbeous, the central pair mostly of this color, on both webs; two outer rectrices with very narrow white tips, 2 mm. deep; bend of wing black; under primary coverts black tipped with white; axillas mostly white; under sides of primaries grayish white on edges of inner webs.

Adult ♀, topotype, No. 37,393, similar in markings to the male, all the colors duller and lateral under tail coverts more noticeably marked with white.

Nestling, topotype, about two-thirds grown, auricular patch olive yellow; head, back, and throat dusky olive green, darkest on top of head and sides of throat; a blackish line down middle of belly; sides, flanks, and under tail coverts dull olive yellow; wings grayish hair brown, scapulars and lesser coverts dull grayish olive, tips of greater coverts yellowish, forming a wing bar; primaries and secondaries edged with greenish gray; tail grayish hair brown edged with greenish gray, outer rectrices *barely* tipped with whitish.

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[1] Named in honor of Dr. Leonhard Stejneger.

Measurements. — Adult ♂ type, wing 62; tail 55.5; tarsus 18.2; exposed culmen 11. Adult ♀, topotype, No. 37,393, wing 60; tail 50; tarsus 18; exposed culmen 10.5.

Corvus macrorhynchus levaillantii (Lesson).

Four specimens, all from Ishigaki, adult ♂ March 25, adult ♀ March 28, and two young from the nest June 10. [Eggs, four in a clutch, were taken April 11 to June 10.]

Sturnia pyrrhogenys (Temm. & Schl.).

One male from Ishigaki, June 1, 1899.

Zosterops loochooensis (Tristram).

Two specimens from Ishigaki, adult ♂ March 13, adult ♀ April 6. [Abundant on Ishigaki and Kuroshima. Skins were taken from February 18 to June 7, and eggs, four in a clutch, April 2 to June 25.]

A careful comparison of these two specimens with numerous examples of *Z. simplex* and *Z. japonica* proves the Liu Kiu form to be a distinct island race, in spite of the doubts cast upon it in the latest review of the group.[1] But as no adequate description of it appears to have been published, I append the following: —

Characters. — Nearest to *Z. simplex* of China, but bill heavier, wing longer; of a brighter green color above, and brighter yellow color below; the species differs from *Z. japonica* in slightly shorter wing and in the color of the sides and flanks, which lack the strong vinous brown of this region in the Japanese species, and also in the primaries, being very short and narrow at tips (a character presented by many of the species of birds peculiar to the Liu Kiu Islands); wing formula, 1st primary about equal to 6th, shorter than 5th, 2nd equal to 4th, 3rd longest.

Color. — Whole upper parts including margins of wing and tail feathers yellowish oil green, frontal region slightly yellower; wings and tail black (except for the green margins of the feathers); orbital ring silky white; a dusky spot below and in front of eye; chin and throat lemon yellow; breast and belly soiled whitish, faintly washed with yellowish along median line and with pale écru drab on sides and flanks; thighs yellowish white in front, dusky oil green behind; under tail coverts lemon yellow; bend of wing lemon yellow; alula black; lining of wing and axillas pale yellow; narrow inner margins to wing feathers below whitish.

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[1] Finsch, O. Zosteropidae. Das Tierreich, 1901, 15, p. 20.

Measurements. — Adult ♂, No. 37,390, wing 57; tail 39.5; tarsus 18; exposed culmen 11.2; distance from tip of longest secondary to tip of longest primary 11.

Adult ♀, No. 37,391, wing 57; tail 40; tarsus 18; exposed culmen 11; distance from tip of longest secondary to tip of longest primary 11.5.

Emberiza spodocephala Pall.

One male, not in full plumage, from Ishigaki, April 8.

Passer montanus saturatus Stejn.

One adult ♂ from Ishigaki, June 30. This specimen differs from the type of *P. saturatus* only by slightly paler colors, due to the more abraded condition of its plumage. [The bird was common in the island, and was breeding in the roofs of the houses. Eggs, seven in a clutch, were taken March 20 to June 25.]

Coccothraustes coccothraustes japonicus (Temm. & Schl.).

One female from Ishigaki, March 7.

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Bulletin of the Museum of Comparative Zoölogy
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DESCRIPTIONS OF NEW AND LITTLE-KNOWN MEDUSÆ FROM THE WESTERN ATLANTIC.

BY ALFRED GOLDSBOROUGH MAYER.

WITH SIX PLATES.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
JUNE, 1900.

No. 1. — *Descriptions of New and Little-known Medusæ from the Western Atlantic.* By Alfred Goldsborough Mayer.

LIST OF SPECIES.

SCYPHOMEDUSÆ.

Bathyluca solaris, nov. gen. et sp.

HYDROMEDUSÆ.

Bougainvillia Gibbsi, nov. sp.
Lymnorea borealis, nov. sp.
Oceania carolinæ, nov. sp.
Oceania singularis, nov. sp.
Octonema gelatinosa, nov. sp.
Orchistoma tentaculata, nov. sp.
Stomotoca apicata, L. Agassiz.
Stomotoca rugosa, nov. sp. = **Stomotoca apicata**, Fewkes.
Syndictyon angulatum, nov. sp.

CTENOPHORÆ.

Mnemiopsis McCradyi, nov. sp.

The Medusæ described in the following paper were obtained by the author as assistant to Mr. Alexander Agassiz in collecting new material for a work upon the Medusa-fauna of the Atlantic Coast of North America. The descriptions of Western-Atlantic Medusæ herein given will eventually be published also in the new edition of The North American Acalephæ now in preparation by A. Agassiz and A. G. Mayer.

Eight species are new; of these one is a Scyphomedusa, one a Ctenophore, and six are Hydromedusæ. In addition to these there is one Hydromedusa (Stomotoca rugosa) that we have redescribed under a new name.

The Scyphomedusa (Bathyluca solaris) is, judging from its structural affinities, a deep-sea type, although the single specimen from which our figures were obtained was found upon the surface of Narragansett Bay, Rhode Island.

The Medusæ described in this paper were collected at different times at Eastport, Maine; Newport, Rhode Island; Charleston, South Carolina; and in the Bahama Islands during visits made to the above localities at the suggestion of Mr. Agassiz.

SCYPHOMEDUSÆ.

BATHYLUCA, nov. gen.

Bathyluca solaris, nov. gen. et sp.

Figs. 1, 2, Plate 1.

A single specimen of a new genus of Discomedusa belonging to the family Ephyridæ was found in Narragansett Bay, Rhode Island, on July 27, 1896, by R. W. Hall, Esq. The medusa was found floating upon the surface, but as it was very much torn and battered, and as it differs widely from any of the hitherto known pelagic medusæ of our coasts, we are inclined to suspect that it may prove to be a deep-sea form, a specimen of which has wandered to the surface.

Generic Characters. — Bathyluca, nov. gen. Discomedusæ with a simple cruciform, central mouth opening, without mouth-arms or palps. There are 16 wide, radial, gastro-vascular pouches (8 ocular and 8 tentacular). There is no ring canal. There are 8 marginal sense-organs and 16 marginal tentacles. There are 4 gonads in the oral floor of the disk, and there are 4 sub-genital pits.

Specific Characters. — The umbrella is flat, and the gelatinous substance is quite thick. It is 45 mm. in diameter, and about 10 mm. in height. The aboral surface of the umbrella is sprinkled over with small clusters of nematocysts. There are 8 marginal sense-organs that are deeply sunken within small niches between the lappets. The entoderm of these sense-organs contains no pigment, but instead there are small white granules (Figure 2). There are 24 marginal lappets and 16 long hollow tentacles. The mouth opening is cruciform in shape, and there appear to be no mouth-arms or palps. We may, however, be mistaken in regard to this, for our specimen was much torn and battered, and it is possible that the palps may have disappeared. There are 4 wide sub-genital pits. The gonads are found in the entoderm of the lower floor of the gastro-vascular cavity, and their position is marked by 4 horseshoe-shaped ridges upon the lower floor of the sub-umbrella. There are a number of long gastric cirri that arise from the regions of the gonads and project slightly beyond the mouth opening. The stomach is large, its diameter being about ½ that of the umbrella itself. Sixteen wide, simple radial pouches extend outward from the stomach cavity into the peripheral regions of the umbrella. Eight of these pouches go to the marginal sense-organs, and 8 to the tentacles which are hollow throughout almost their entire length. There are 8 radial bands of muscle fibres in the ex-umbrella. These go to the marginal sense-organs. The gelatinous substance of the disk is translucent but slightly bluish in color. The clusters of nematocysts over the aboral surface are dull yellowish brown, and the tentacles are slightly green in color.

Single specimen, Narragansett Bay, Rhode Island.

HYDROMEDUSÆ.

STOMOTOCA, L. AGASSIZ, 1862.

Stomotoca apicata, L. AGASSIZ.

Fig. 3 ♂, Fig. 4 ♀, Plate 2.

Male	Saphenia apicata, McCrady, J., 1857, Gymn. Charleston Harbor, p. 27, Pl. VIII. Figs. 2, 3. Stomotoca apicata, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 347. Stomotoca apicata, Agassiz, A., 1865, North Amer. Acal., p. 168.
Female	Dinematella cavosa, Fewkes, J. W., 1881, Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. VIII. p. 151, Pl. II. Figs. 2, 3; Pl. IV. Fig. 3. Dinematella cavosa, Fewkes, J. W., 1884, Amer. Nat., Vol. XIX. p. 195, Fig.

Stomotoca apicata, L. Agassiz, is distinguished by the fact that the entoderm of the proboscis in the male is emerald green, or straw-colored; and in the female dull ochre. Also the tentacle bulbs in the male are purple, and in the female dull ochre. This species has been confounded by Brooks, 1883, and Fewkes, 1881, with another form in which the entoderm of the proboscis and tentacle bulbs is brick-red in both sexes. For this brick-red form we propose the name Stomotoca rugosa.

Specific Characters. — Stomotoca apicata. In the adult medusa the bell is about 4 mm. high and 2 mm. broad. It is provided with a prominent apical projection that is solid in the males, but usually hollow in the females, the gastro-vascular space leading upward into it. There are two long tentacles with large, hollow basal bulbs. In addition to the two long tentacles there are usually 6 small rudimentary tentacle bulbs upon the bell margin. The proboscis is flask-shaped, there is no peduncle, and the 4 lips are curved slightly upward. The ectoderm of the upper portion of the proboscis, under the 4 radial tubes, is thrown into folds or convolutions, and it is in this region that one finds the gonads. There are 4 broad radial tubes and a broad circular vessel with somewhat jagged outlines. The velum is well developed. The color of the proboscis in the male varies from intense green to dull ochre-yellow, or cream-color; and the basal bulbs of the tentacles vary from faint to deep purple. In the females, the proboscis and tentacle bulbs are usually dull ochre-yellow, or cream-color, but in some few individuals the proboscis is faintly straw-colored, and the tentacle bulbs faint purple. In the female the apical projection of the bell is hollow, while in the male it is usually solid.

Common at Newport, Rhode Island, from July 15–September. Rare at Charleston, South Carolina.

The young medusa resembles the adult excepting that the apical projection to the bell is wanting, or is but little developed. There are 2 tentacles and 2 rudimentary tentacle bulbs. The sexual color difference is seen in the youngest medusæ we have observed. The hydroid stock is unknown.

Stomotoca rugosa, nov. sp.

Fig. 5, Plate 2.

Stomotoca apicata, Fewkes, J. W., 1881, Bull. Mus. Comp. Zoöl., Vol. VIII. p. 152, Pl. II. Figs. 1, 4, 9.

Amphinema apicatum, Brooks, W. K., 1883, Studies Biol. Lab. Johns Hopkins Univ., Vol. II. p. 473.

The bell is 5 mm. high and 3 mm. broad; it bears an apical projection which in some specimens is long and slender, and in others is short and blunt. The substance of this projection is solid throughout. There are 2 long, well-developed tentacles and 14 small rudimentary ones. The basal bulbs of the long tentacles are large and hollow. When fully stretched, the long tentacles attain a length of 4–6 times the bell height. The velum is well developed. There are four broad radial tubes, and a broad circular vessel with jagged outlines. The proboscis is flask-shaped, the lips being flanged and quite prominent. The sexual products are found in the ectoderm of the upper portion of the proboscis where the outer surface is folded into a complex series of ridges. The bell is transparent, and the entoderm of the tentacle bulbs and of the proboscis is brick-red. In some individuals the 4 radial tubes and the circular vessel are faint red.

There is a well-marked southern variety of this species, found at the Tortugas, Florida, in which the proboscis and the tentacle bulbs are brick-red streaked with black. In some individuals, indeed, the proboscis and tentacle bulbs are coal-black.

Brooks, 1883, has described the hydroid and young medusa of this species from Beaufort, North Carolina. According to him, the hydroid stock is a Perigonimus very much like P. minutus, Allman, 1871, p. 324, Plate XI. Figures 4–6.

This medusa is common at Newport, Rhode Island, and is also found at Charleston, South Carolina. It is rare at the Tortugas, Florida.

SYNDICTYON, A. AGASSIZ, 1862.

Syndictyon angulatum, nov. sp.

Figs. 6-8, Plate 3.

Specific Characters. — The bell is almost square in cross-section and is not quite as broad as it is high. The bell height in the specimens found by us was about 2.5 mm. There are 4 stiff tentacles that are about three-fourths as long as the bell height. The distal halves of these tentacles are conical in shape, and are covered thickly with clusters of nettle cells. The basal bulbs of the tentacles are large and swollen, and contain each a single well-developed ectodermal ocellus. This ocellus is formed by a cup-shaped invagination of ectodermal cells that are deeply stained with dark-brown pigment granules. It is probable that this structure constitutes a very primitive udoscopic eye. The velum is small. There are 4 narrow, straight, radial tubes and a slender circular vessel. The proboscis is spindle-shaped, and the mouth is a simple circular orifice. The gonads are situated within the ectoderm of the proboscis. The entoderm of the proboscis and of the tentacle bulbs varies from turquoise to blue-green in different specimens.

Several specimens of this medusa were found off Turks Islands, Bahamas, January 20, 1893.

BOUGAINVILLIA, LESSON, 1836.

Bougainvillia Gibbsi,[1] nov. sp.

Figs. 14, 15, Plate 4.

Specific Characters. — Adult medusa ; Figure 14. The bell is about 4 mm. in height and 3.8 mm. in diameter. The gelatinous substance is very thick, so that the bell cavity is only about one half as deep as the height of the animal. There are 4 clusters of marginal tentacles which arise from 4 large bulbous swellings, situated at the bases of the 4 radial canals. Each bulbous swelling gives rise to 4 or 5 long slender tentacles. There is a single dark-brown ocellus at the base of each tentacle upon the centripetal (lower) side. The velum is small. There are 4 straight, narrow, radial canals. The proboscis is wide and cruciform in cross-section, and the radial canals arise from the 4 corners of the cross. The proboscis is short and does not extend quite one half the distance from the inner apex of the bell cavity to the velar opening. The mouth is situated at the extremity of a short tubular neck, and there are no prominent lips. Four radially situated oral tentacles arise from the sides of the neck of the proboscis. Each one of these branches dichotomously about twice. The gonads are developed upon the sides of the stomach, and in the female the ova are large and prominent. The proboscis is pearl-colored, or of a delicate green. The entodermal cores of the tentacle bulbs are red surrounded by a delicate yellow-green. The supporting lamella of the bell often displays a faint greenish tinge.

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[1] Named for Mrs. Theodore K. Gibbs.

Young Medusa. — In the young medusa there are but 8 tentacles, 2 from each tentacle bulb. The bell is a little higher than a hemisphere and the gelatinous substance is not very thick, being of about uniform thickness everywhere instead of being very thick at the aboral pole, as in the adult. The proboscis is short and quadratic, and there are 4 short, unbranched, knob-shaped oral tentacles. When the medusa is about 3 mm. in height, the bell is still hemispherical. The proboscis is wide, shallow, and quadratic, and the oral tentacles branch once dichotomously. About 4–5 marginal tentacles arise from each tentacle bulb.

This medusa is found in Newport Harbor, Rhode Island, from July until October.

This species is distinguished from Margelic carolinensis, L. Agassiz, by the greater height and less width of its bell. Also in M. carolinensis the proboscis is long and slender, while in B. Gibbsi it is short, wide, and cruciform in cross-section. The proboscis of M. carolinensis is widest at about the middle point of its length, while that of B. Gibbsi is widest at its proximal base.

LYMNOREA, Péron and Lesueur, 1809.

Lymnorea borealis, nov. sp.

Figs. 16–18, Plate 5.

Specific characters. — The bell is 3 mm. in height. The bell walls are thin, and there is a slight apical projection. There are 32 well-developed marginal tentacles with large basal bulbs. These tentacles are about ½ as long as the bell height, and are curled slightly upward. They are not very flexible. The velum is well developed. There are 4 straight, narrow radial tubes. The proboscis is pyriform and the mouth is surrounded by 4 short, dichotomously branching, oral tentacles. Each of these oral tentacles branches 2 times, thus giving rise to 4 tentacle tips (see Figure 18). These tips are short and knob-like and are covered with long slender nematocyst capsules borne upon thread-like filaments (see Figure 17). The gonads occupy 4 radially situated, longitudinal swellings upon the proboscis. The entoderm of the proboscis, and of the bulbs of the marginal tentacles, is red.

Three specimens, all of them being males, were found in Eastport Harbor, Maine, on September 19, 1898.

OCEANIA, Péron and Lesueur, 1809.

Oceania carolinæ, nov. sp.

Figs. 9-11, Plates 3, 4.

Specific Characters. — The bell is not quite a hemisphere, and is 14 mm. in diameter. The cavity of the bell is shallow, so that the gelatinous substance is quite thick. There are 16 well-developed marginal tentacles with large, hollow basal bulbs. These are only about half as long as the bell diameter, but as they are usually carried coiled in a close helix they appear much shorter. In addition to these well-developed tentacles there are 48 small rudimentary tentacle bulbs that probably never develop into tentacles. There are 64 otocysts, 4 between each adjacent pair of large tentacles (see Figure 11). Each otocyst contains 2 spherical otoliths. The velum is well developed. There are 4 narrow, straight, radial canals. The mature proboscis (Figure 10) is flask-shaped, and there are 4 simple curved lips. The gonads are developed upon the radial tubes at about one quarter the distance from the circular vessel to the proboscis. In the female the ova are very conspicuous. The entoderm of the tentacle bulbs and proboscis and of the radial tubes in the region of the gonads is bright yellow-green.

This species was extremely abundant in Charleston Harbor in the early part of September, 1897, and in June, 1898.

Oceania singularis, nov. sp.

Figs. 12, 13, Plate 4.

Specific Characters. — The bell is 2 mm. in diameter and the sides are quite straight and sloping. Near the apex of the bell there is a sharp constriction, above which there is a lens-shaped apical projection. There are 16 well-developed marginal tentacles with large, hollow, conical-shaped basal bulbs. The lashes of the tentacles are short and are covered with nematocystic cells. In addition to the 16 functional tentacles there are 16 intermediate rudimentary ones. There are 32 otocysts, each containing a single highly refractive spherical otolith. There are 4 straight radial tubes. The proboscis is quadrangular in cross-section, and there are 4 simple lips. The 4 gonads are developed upon the 4 radial canals near the base of the proboscis. The entoderm of the proximal part of each tentacle bulb is turquoise-green, and the distal part is brownish-red. The entoderm of the proboscis and of the radial tubes in the neighborhood of the gonads is of a delicate turquoise tinge.

A single specimen of this medusa was found in Newport Harbor, Rhode Island, on August 22, 1896.

OCTONEMA, HAECKEL, 1879.

Octonema gelatinosa, nov. sp.

Figs. 20, 21, Plate 6.

Specific Characters. — Young medusa? The bell is 3.5 mm. in diameter and somewhat flatter than a hemisphere. The gelatinous substance is quite thick. In the single specimen examined there were 4 tentacles with long hollow basal bulbs. These tentacles were about 2 times as long as the bell diameter. Within the entoderm of the inner side of each tentacle bulb there was a single dark-colored pigment spot. In addition to these long tentacles there were 12 rudimentary tentacle bulbs upon the bell margin. It is possible that these might have in time developed tentacles; in the specimen observed by us, however, they were very small and apparently rudimentary. A dark-colored pigment spot was found in the entoderm of each of these tentacle bulbs. There were 8 marginal clubs, 2 in each quadrant. A dark-brown entodermal pigment spot was situated at the base of each (see Figure 21). The velum was well developed. There were 4 straight radial canals upon the upper regions of which the gonads were situated. The proboscis was a simple tube with 4 simple lips. The color of the entoderm of the 4 large tentacle bulbs, and of the radial tubes in the region of the gonads was green.

A single specimen was found in Charleston Harbor, South Carolina, September 14, 1897.

ORCHISTOMA, HAECKEL, 1879.

Orchistoma tentaculata, nov. sp.

Fig. 19, Plate 5.

Specific Characters. — Young medusa: The bell was 6 mm. in height. The sides near the margin were slightly flanged outward. The gelatinous substance of the upper portion of the bell was very thick, so that the concavity was shallow. There were thirty-two marginal tentacles in various stages of development, the longest being about 1.5 times as long as the bell height. The tentacles possessed long, hollow basal bulbs. There were no marginal sense-organs. There were sixteen functional radial tubes, and sixteen others in process of development. The radial tubes were straight, and there were no traces of gonads upon them. The velum was well developed. The proboscis was flat and shallow, and there were 8 lips. The entoderm of the basal bulbs of the tentacles was of a delicate green. Only one immature specimen of this medusa has ever been seen; it was found at Newport, Rhode Island, August 18, 1896. The genus is closely related to Melicertum.

CTENOPHORÆ.

MNEMIOPSIS, L. AGASSIZ, 1860.

Mnemiopsis McCradyi,[1] nov. sp.

Figs. 22, 23, Plate 6.

Specific Characters. — Mnemiopsis McCradyi: This species is closely allied to Mnemiopsis Leidyi, A. Agassiz, but differs from it chiefly in the much greater complexity of the ramifications of the chymiferous tubes within the lappets; and also in the very decided amber color of the gelatinous substance of the animal. It is also remarkable that in this species the gelatinous substance of the body is of so tough a nature that the creature may be removed from the water by hand without suffering injury. Indeed, we know of no Ctenophore that is as resistant as this species. The animal is 100 mm. in length, our figures being natural size. There are eight longitudinal rows of ciliated plates. Four of these rows, that extend down the lateral lappets, are about twice as long as are the four others that lead from the apex to the auricles. The body is markedly compressed, the broad lateral axis, extending through the lappets, being about twice as great as the auricular axis. (Compare Figures 22 and 23.) The lateral lappets are about as long as the remaining portion of the body, and are similar in shape and size to those of M. Leidyi, and much longer than in M. Gardeni. (See A. Agassiz, 1865; North American Acalephæ, Figures 20, 21 and 22, 23.) The apical sense-organ is found at the bottom of a deep cleft at the aboral pole of the body, and is similar in structure to that of M. Leidyi. The chymiferous tubes that wind through the lateral lappets are of a decided purple color and their ramifications are very complex. The mature ova are similar in appearance to those of M. Leidyi.

A single perfect specimen of this species was found in Charleston Harbor, South Carolina, September 15, 1897.

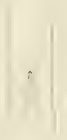
---

[1] This species is named in honor of Professor John McCrady in recognition of his important researches upon the medusæ of Charleston Harbor.

PLATE 1.

Fig. 1. Bathyluca solaris, nov. gen. et sp. Oral view of the medusa.
Fig. 2. Bathyluca solaris. Oral view of one of the marginal sense-organs.

2



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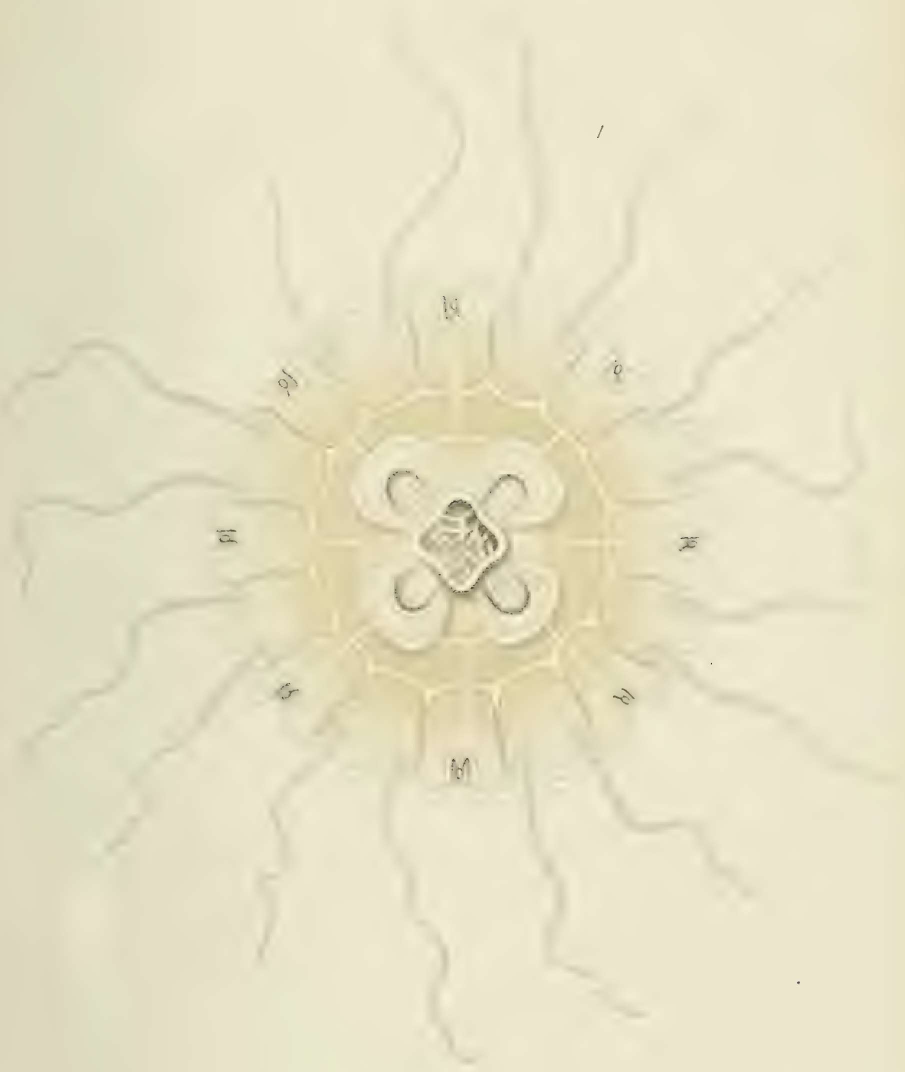

B. Meisel lith. Boston

PLATE 2.

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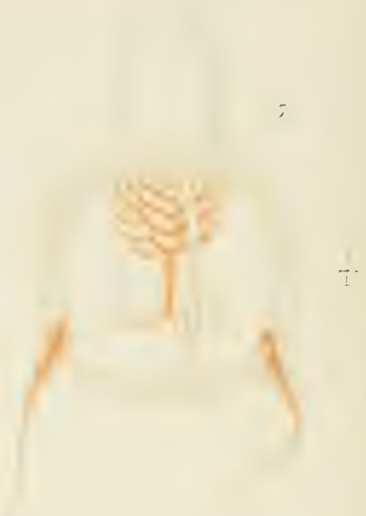
Fig. 4. Stomotoca apicata. Female medusa.
Fig. 5. Stomotoca rugosa, Mayer = Stomotoca apicata, Fewkes, 1881.



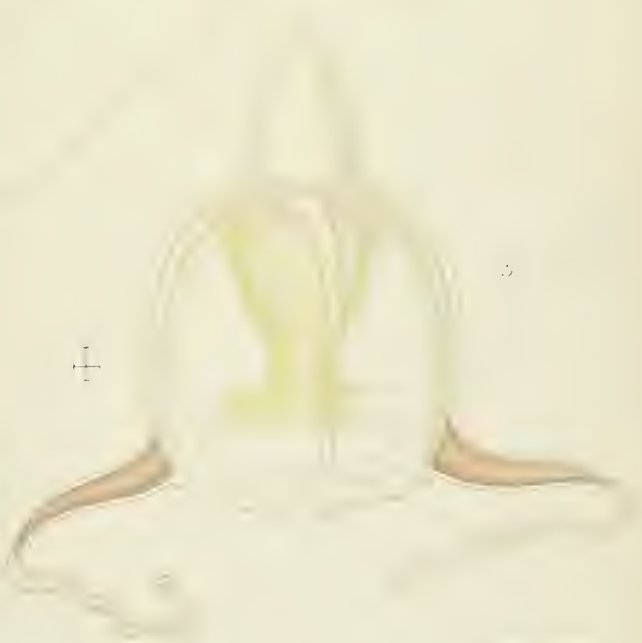


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PLATE 3.

Fig. 6. Syndictyon angulatum, nov. sp. Side view of medusa.

Fig. 7. Syndictyon angulatum. Side view of one of the tentacle bulbs, showing the ocellus.

Fig. 8. Syndictyon angulatum. Surface view of tentacle bulb.

Fig. 9. Oceania carolinæ, nov. sp.

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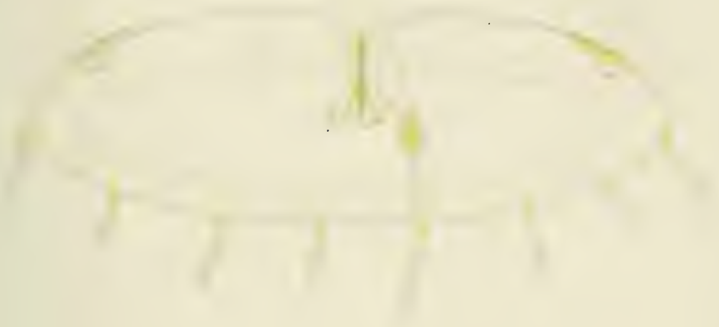

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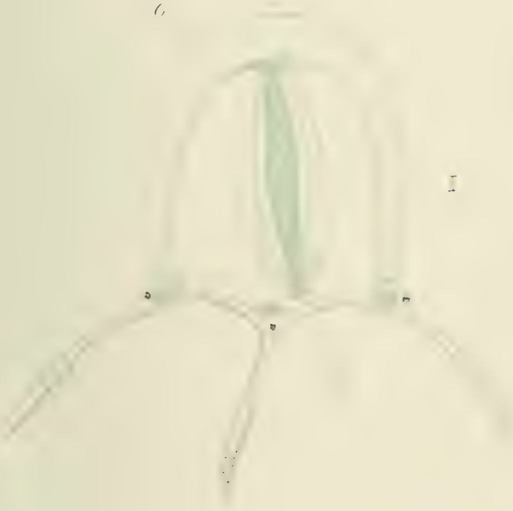

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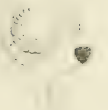

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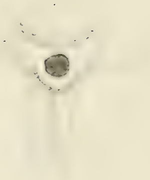

E. Meisel lith Boston

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Fig. 15. Bougainvillia Gibbsi, nov. sp. Young medusa.

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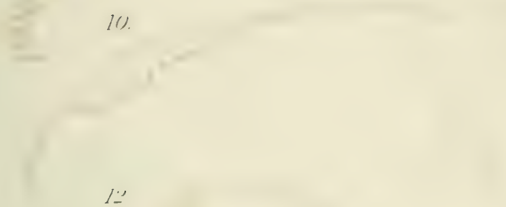
10.



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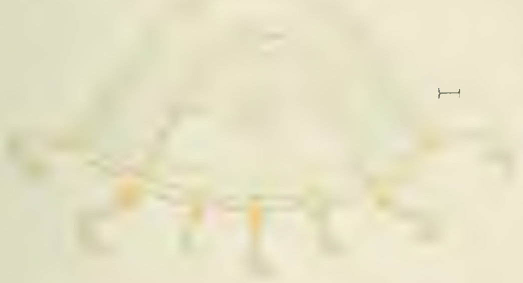

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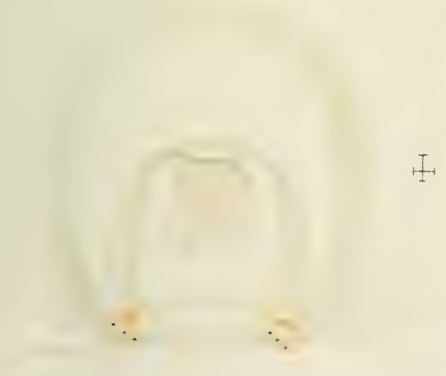

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B. Meisel lith. Boston.

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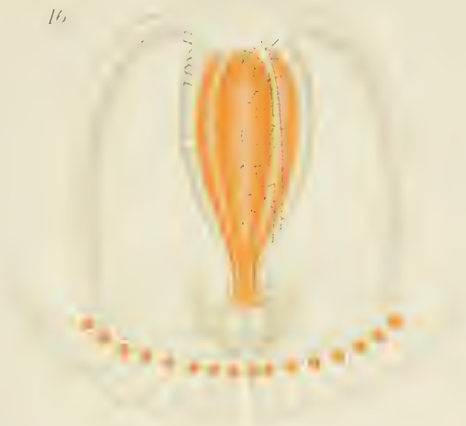
Fig. 19. Orchistoma tentaculata, nov. sp.

16.



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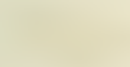

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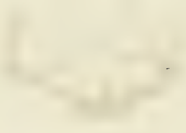

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PLATE 6.

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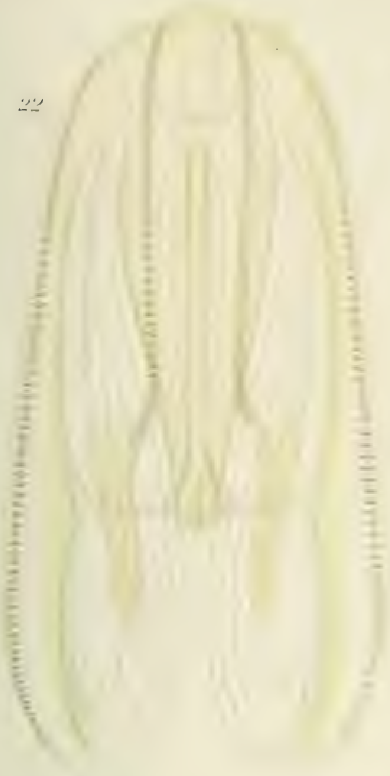

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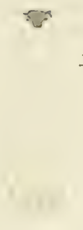

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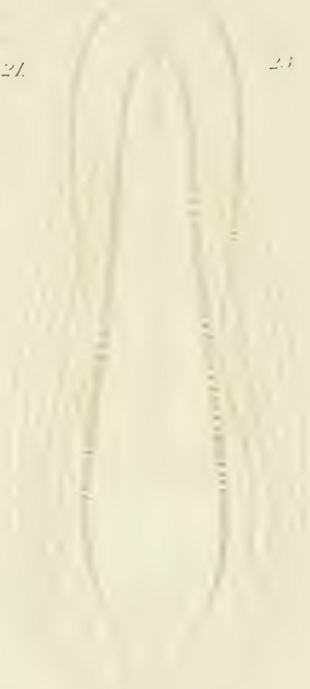

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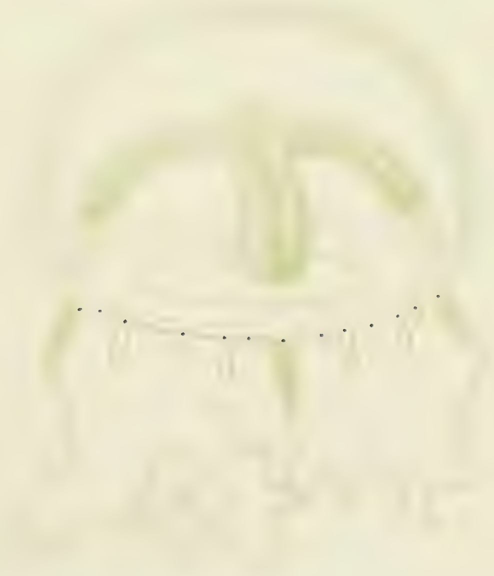

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B Meisel lith Boston

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AT HARVARD COLLEGE.
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SOME MEDUSÆ FROM THE TORTUGAS, FLORIDA.

By Alfred Goldsborough Mayer.

With Forty-four Plates.

CAMBRIDGE, MASS., U.S.A.:
PRINTED FOR THE MUSEUM.
July, 1900.

No. 2. — *Some Medusæ from the Tortugas, Florida.* By ALFRED GOLDSBOROUGH MAYER.

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INTRODUCTION.

The medusæ described in the following paper were obtained by the author while assistant to Mr. Alexander Agassiz in collecting for a work upon the Medusa fauna of the Atlantic Coast of North America. Three expeditions were made, for Mr. Agassiz, to the Tortugas, Florida, extending from June 10–22, 1897; June 25–August 19, 1898; and May 14–July 4, 1899. The manuscript has been submitted to him, and the descriptions herein given will ultimately be published also in the new edition of "North American Acalephæ" now in preparation by A. Agassiz and A. G. Mayer.

We wish to avail ourselves of this opportunity to express our appreciation of the cordiality and kindness of George R. Billbury, Esq., head keeper of the lighthouse at Loggerhead Key, Tortugas, to whose intelligent and painstaking co-operation we owe much that may be of value in the following paper. We also wish to thank Major J. E. Sawyer, U. S. A., to whose permission we were indebted for the use of the government steamer, "George W. Childs," for transportation to and from between Key West and the Tortugas. We are also indebted for a like service to the officers of the Union Bridge Company in allowing the use of their steamer "Ambrosio Bolivar."

The Tortugas occupy what is probably the most favorable situation from which to study the pelagic life of the Tropical Atlantic. They lie upon the northern edge of the deep channel of the Gulf Stream as it issues from the Gulf of Mexico. Pure, deep ocean water surrounds them, and there are none of the shallow mud-flats that render the shore waters of Florida so turbulent, at times, that many of the more delicate pelagic animals are killed. As is well known, the Gulf Stream pours outward from the Gulf of Mexico through the Straits of Florida. The Gulf Stream does not occupy the whole cross-section of the strait, however, but according to the researches of Lieutenant, now Commander, J. E. Pillsbury (Report U. S. Coast and Geodetic Survey, 1885–87), it flows nearer to the Cuban coast than to the line of the Florida Keys. The northern limit of this great stream lies at least 28 miles south of Rebecca Shoal, the average edge being about 6 miles farther south, or 34 miles south of Rebecca Shoal (see U. S. Coast Survey Report, 1887, pp. 174, 175, Illustration 42).

The currents in the immediate vicinity of the Tortugas are extremely variable and are greatly under the influence of the tides and winds, while the tides themselves are small and easily influenced by extraneous circumstances. In the passage between Rebecca Shoal and the Tortugas the current sets practically north with the flood tide and south with the ebb. About five miles west of Loggerhead Key the southerly set of the ebb tide is stronger than the northerly current induced by the flood. There can be no doubt that the prevailing winds play an important part in setting up local currents in the immediate vicinity of the Tortugas. The prevailing E.–S.E. winds of the summer months cause a decided westerly surface drift, and this is evidenced by the fact that during this period sand is washed away from the eastern shore of Loggerhead Key and spread out into long cuspate forelands[1] which extend from both the north and south ends of the island in a westerly direction. The island thus assumes, roughly, the form of a crescent with its horns pointing westward. The north winds that occur during the winter months annually destroy these crescentic horns, but they are annually replaced by the summer breezes.

---

[1] "Cuspate foreland" is a term used by F. P. Gulliver (1896; Bull. Geol. Soc. America, Vol. VII.) to denote a sandy, projecting point of land which has cuspate outlines, and is formed by the agency of currents.

Although the northern edge of the *current* of the Gulf Stream probably never impinges against the Tortugas, a fresh south breeze is sufficient to drive its surface waters, unaccompanied by the current,[1] upon the islands, and under these conditions vast quantities of gulf-weed, and large numbers of Physalia, Velella, and other pelagic animals are cast up upon their shores. It is well known that the Gulf Stream bears along upon its surface vast numbers of floating animals that are drawn into it by winds and currents from the adjacent tropical regions of the Atlantic, and thus it comes about that pelagic animals from all over the Gulf of Mexico and West Indies are drifted past the Tortugas.

The temperature of the surface waters in the immediate vicinity of the Tortugas is remarkably high, being about 74°–77° F. in winter, and 80°–86° F. in summer, the average for the whole year being about 78° F. It is probably owing to this high temperature, and also to the great purity of the ocean water, that marine animals may be maintained alive in aquaria with remarkable success at the Tortugas; for the temperature of the laboratory is almost sure to be lower than that of the sea, and thus the animals in the aquaria are refreshed and thrive well.

Comparison of the Tortugas Fauna with that of the Southern Coast of New England.

Ninety species of Acalephs have been found at the Tortugas. Of these, 62 are Hydromedusæ, 16 Siphonophoræ, 7 Scyphomedusæ, and 5 Ctenophoræ. Of these, 39 species are new to science, 33 being Hydromedusæ, 3 Siphonophoræ, 1 Hydroid, and 2 Scyphomedusæ.

The Acalephian fauna of the Tortugas is strictly tropical, and is totally different from that of the eastern coast of New England north of Cape Cod. A number of characteristic Tortugas forms are, however, blown northward every summer, and are thus found in considerable numbers upon the southern coast of New England, where they have been found in Newport Harbor and in Buzzard's Bay. Only three Tortugas species have, however, succeeded in establishing themselves in Buzzard's Bay and Newport Harbor; these are: Turritopsis nutricula, Margelis carolinensis, and Stomotoca rugosa. But these northern specimens of the two latter forms display distinct and constant color differences which distinguish them from their near relatives in the Tortugas, and probably entitle them to rank as varieties one of the other. In addition to these three Hydromedusæ, there is one Scyphomedusa, Dactylometra quinquecirra, that is established in Tampa Bay, Florida, and also in the bays and estuaries of the southern coast of New England. It has not yet been found at the Tortugas, but, judging from its range of distribution, it probably will be discovered there.

---

[1] See Lieutenant (now Commander) J. E. Pillsbury, 1886, Report of U. S. Coast and Geodetic Survey, Appendix No. 11, p. 287.

There are a number of other characteristic Tortugas Acalephs that may be classed as occasional visitors to the southern coast of New England, upon which they are drifted by the agency of the prevailing S.–S.W. winds of the summer months. None of these appear to succeed in establishing themselves permanently upon the New England coast. Among these Hydromedusæ may be mentioned, Eutima mira, Æquorea floridana, Glossocodon tenuirostris, and Liriope scutigera; and among the Siphonophoræ, Physalia pelagica, Velella mutica, Porpita Linnæana, Diphyes bipartita, Eudoxia campanula, Ersæa Lessonii, Diphyopsis campanulifera, and Diplophysa inermis. No doubt further researches will increase this list of tropical Acalephs that are drifted far from their southern habitat and slowly perish in the colder waters of the north.

It is interesting to notice that the Acalephian fauna of Charleston Harbor, South Carolina, in latitude 32°, 20′, is very different from that of the Tortugas, and may be said to be subtropical; for it is intermediate in character between the fauna of the Tortugas and that of the southern coast of New England. For example, the following 13 Acalephs are established both at Charleston, South Carolina, and on the southern coast of New England: Dactylometra quinquecirra, Cyanea versicolor, Eucheilota duodecimalis, Epenthesis bicophora, Oceania languida, Willia ornata, Gemmaria gemmosa, Pennaria tiarella, Stomotoca rugosa, Stomotoca apicata, Turritopsis nutricula, Margelis carolinensis, and Nemopsis Bachei; and the following 17 Acalephs are found both at Charleston and the Tortugas: Dactylometra quinquecirra? Beroë Clarkii, Bolina vitrea, Margelis carolinensis, Stomotoca rugosa, Gemmaria gemmosa, Turritopsis nutricula, Halitiara formosa, Æquorea floridana, Eutima mira, Eutimalphes cœrulea, Epenthesis folleata, Eucheilota ventricularis, Steenstrupia gracilis, Liriope scutigera, Glossocodon tenuirostris, and Dyscannota gemmifera. In addition to these there are a few Acalephs such as Stomolophus meleagris that are strictly subtropical, having been found neither at the Tortugas nor upon the southern coast of New England, but which are abundant at Charleston.

It is important to observe, also, that the Acalephian fauna of the Bermudas, like that of Charleston, is distinctly intermediate between the fauna of the Tortugas and that of the southern coast of New England. Of the 30 species described from the Bermuda Islands by Fewkes (1883; Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XI.), 9 are established at Newport, Rhode Island; and 16 at the Tortugas.

Not a single species of acaleph known from the Tortugas has been found established upon the eastern coast of New England north of Cape Cod. The fauna of the eastern coast of New England is, however, closely related to that of the northern coast of Europe (see Browne, 1895, Trans. Liverpool Biol. Soc., 96; Proc. Zoöl. Soc., London; Hartlaub, 1897; Helgolands Medusen, etc.).

To summarize, then, we have at the Tortugas a tropical fauna that gradually disappears, and is replaced by other forms, as we go northward along the coast of the United States. Only three species of the Tortugas fauna are established upon the southern coast of New England, and not one extends north of Cape Cod, Massachusetts. It appears that the great majority of the forms established at the Tortugas are incapable of surviving in the colder waters of the north, although individuals are annually driven far to the northward of their natural habitat by the agency of the Gulf Stream, and the prevailing S.-S.W. winds of the summer season.

COMPARISON OF THE TORTUGAS FAUNA WITH THAT OF THE TROPICAL ATLANTIC.

Very instructive facts are brought to light when we compare the Acalephian fauna of the Tortugas with that of the warm zone of the Atlantic Ocean. By the term "warm zone" we include all that region of the Atlantic lying between 30° N. Lat. and 10° S. Lat., and extending from the coast of Africa to the American shores. This "warm zone" includes the Canary and Cape Verde Islands, the Bahamas and West Indies, the Guinea Stream, the North and South Equatorial Currents, and the warmer parts of the Gulf Stream. At the present time about 130 species of Hydromedusæ are known to inhabit this "warm zone."

Haeckel, 1879, describes 30 species from the Canary Islands, 10 from the coast of Africa and Cape Verde Islands, and 10 from the "Tropical Atlantic." Maas, 1893, in his account of the Hydromedusæ of the Plankton Expedition, enumerates about 21 additional species; and 57 others have been made known by L. Agassiz, Brooks, Fewkes, and Mayer from the Bahamas, Florida Reefs, and Tortugas.

The Hydromedusan fauna of the Tortugas is so closely related to that of the Florida Reefs and the Bahama Islands, that they may be said to be practically identical; and we will therefore speak of it hereafter as the "Bahama-Tortugas" fauna.

When we come to compare the Hydromedusan fauna of the Bahama-Tortugas with that of the remaining portion of the "warm zone," exclusive of the West Indies, we are met with the remarkable fact that only 7 species are known to be common to both the Bahama-Tortugas region and the great remaining region of the "warm zone." Thus only 5 Hydromedusæ have been found in both the Canary Islands and Bahama-Tortugas region. These are Æginella dissonema, Aglaura hemistoma, Aglaura hemistoma var. Nausicaa, Staurodiscus tetrastaurus, and Laodicea ulothrix. Two other Hydromedusæ, Glossocodon tenuirostris and Liriope scutigera, are found in the midst of the ocean between the Canary Islands and the West Indies. It will be noticed that 5 out of these 7 forms that are common to both the eastern and western halves of the "warm zone" are Trachylina, or forms that develop through a free-swimming planula and pelagic actinula stage. The two others, Laodicea ulothrix and Staurodiscus tetrastaurus, belong to the Leptolinidæ and probably develop through a sessile hydroid stage with alternation of generations. In 1893 it was shown by Maas in "Die Craspedoten Medusen der Plankton-Expedition," and in Natural Science, Vol. II. pp. 92–99, that the great majority of the Hydromedusæ found in the midst of the Atlantic, far from land, belong to the Trachylina, and the few Leptolina discovered always show a relation to some neighboring coast. As is well known, it was the avowed object of Hensen's Plankton Expedition of 1889 to study the organic life of the high seas as free from the influence of coasts as possible. This expedition entered the region that we have designated the "warm zone" on August 20, and left it on October 20, 1889. During these two months the expedition remained for by far the greater part of the time upon the high seas, approaching land only at the Cape Verde Islands, Ascension, Fernando Noronha, and the mouth of the Amazon. As has been shown by Maas, 1893, the Hydromedusæ found in this region consisted almost entirely of forms of Trachylina, composed of Trachynemidæ, Aglauridæ, and especially Geryonidæ. (See Craspedoten Medusen der Plankton Expedition, 1893, Taf. VII., VIII.)

The facts then appear to be that we have at the eastern extremity of our "warm zone," or in that region adjacent to the coast of Africa and in the neighborhood of the Canary Islands, a Hydromedusan fauna composed of both Trachylina and Leptolina, and the species which compose this fauna show a distinct relationship with Mediterranean forms. In the midst of the "warm zone," midway between the Canary Islands and the West Indies, the fauna is composed *almost entirely* of forms of Trachylina that are pelagic species *par excellence*, and are distributed widely over the high seas, and also reach the coasts of Africa and America. In the Bahama-Tortugas region we find a Hydromedusan fauna composed of both Trachylina and Leptolina, the Leptolina forms of which are *almost wholly distinct* from those of the Canary Islands.

We wish to call attention to the fact that a comparison of the Hydromedusan fauna of the Bahama-Tortugas with that of the Canary Islands is open to serious objections, and that the conclusions arrived at through such a comparison may be of but little value. The Canary Islands occupy a small area, and are surrounded by water of 1000–2000 fathoms in depth, while the temperature of the surface water in their neighborhood is about 10° F. colder than that of the Bahama-Tortugas region. We might then expect that a marked difference would be observed in the Hydromedusan faunæ of the two regions, for in the neighborhood of the Bahamas and Tortugas we find great areas of very shallow water having a very high temperature, while even the deepest parts of the Gulf of Mexico and Caribbean Sea have a temperature of 39½° F. It would be much fairer and far more conclusive, were we able to do so, to institute a comparison between the fauna of the Bahama-Tortugas and that of the Gulf of Guinea in the neighborhood of the Islands of Anno Bom, St. Thomas, and Fernando Po; for here the continental slope of the African coast is more gradual than at any other place, and the islands are surrounded by a depth of water not greater than 500 fathoms, having a bottom temperature of 39½° F.; which is exactly the same as that of the deep parts of the Gulf of Mexico. The temperature of the surface water is also nearly the same as that of the Bahama-Tortugas region. The conditions at the Tortugas in August and September are very similar to those in the Gulf of Guinea in February and March, as will become clear through an inspection of Krümmel's Temperature Charts (Kettler's Zeitschrift, Bd. VI., Taf. II., III. Also, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XIV., pp. 240, 242, Figs. 168, 169). Unfortunately the Hydromedusan fauna of the Gulf of Guinea is unknown, but when we come to know it, we would not be surprised were it found that many Tortugas forms are established in this region.

The Scyphomedusæ of the Bahama-Tortugas region are, for the most part, distinctly West Indian types, and are quite different from the species found on the Atlantic Coast of Africa. It is well known that these forms are much more abundant along coasts than they are in the open sea. The Discomedusæ, especially, are given to congregating in swarms in bays and estuaries. We are therefore not surprised to find that most of the Bahama-Tortugas species are peculiar to the West Indies and the adjacent warm coasts of North and South America. Vanhöffen (1888; Bibliòtheca Zoologica, and 1892; Acalephen der Plankton Expedition) has given maps showing the geographical distribution of Scyphomedusæ, and from an inspection of his charts it becomes quite apparent how these forms are distributed along coasts, and that few of them have yet been found in the open sea. Indeed, according to Vanhöffen ('92) only six Scyphomedusæ were found by the Plankton Expedition of 1889, which confined its investigations, as far as possible, to the open sea far from coasts.

The following Scyphomedusæ appear to be restricted to the Bahama-Tortugas region and the West Indies: Cassiopea frondosa, Lamarck; Cassiopea xamacana, Bigelow; Linerges mercurius, Haeckel; Linerges pegasus, Haeckel; Linuche ungiculata, Eschscholtz; Linuche vesiculata, Haeckel; Aurelia habanensis, Mayer; Aurelia marginalis, L. Agassiz; Charybdea xamacana, Conant; Tripedalia cystophora, Conant; Charybdea punctata. In addition to these the following forms are established in the Bahama-Tortugas region, but extend also for a considerable distance northward along the coast of the United States: Pelagia cyanella, Péron and Lesueur; Dactylometra quinquecirra, L. Agassiz; Tamoya haplonema, F. Müller. The following species extend from the West Indies southward along the Brazilian coast; Dactylometra lactea, L. Agassiz; Tamoya haplonema, F. Müller.

There are also a few Scyphomedusæ of very wide distribution that are found in the region of the West Indies and Bahamas. Among these are: Nausithoë punctata, Kölliker, found in the Mediterranean, the Tropical Atlantic, and the Bahamas. A very close variety, N.

punctata var. pacifica, occurs in the Tropical Pacific. Periphylla hyacinthina, Steenstrup; found widely distributed throughout the whole Atlantic Ocean (see Vanhöffen, 1892; Akalephen der Plankton Expedition, Taf. V.). Pelagia phosphora, Haeckel; appears to be widely distributed over the Tropical Zone of the Atlantic Ocean (see Haeckel, 1879, p. 507, Vanhöffen, 1892, pp. 19, 20); Atolla Bairdii, Fewkes, is a deep sea form that has been found by the "Albatross" in the Gulf Stream, off the coast of the United States, and by Vanhöffen south of the Cape Verde Islands, off the African coast.

The Siphonophoræ of the Bahama-Tortugas region are almost all widely distributed Tropical Atlantic forms, and most of them have already been found by Haeckel, and by Chun, in the Canary Islands. The Siphonophoræ are pelagic animals *par excellence*, and as they undergo their development while floating within the ocean, and are quite, if not wholly, independent of the bottom, one finds them widely distributed by ocean currents. As was pointed out by Chun (1897, Siphonophoren der Plankton Expedition, p. 101, etc.), the Siphonophoræ of the warm regions of the Atlantic Ocean are widely distributed, distinctive species not being confined to particular regions. It is quite true, however, as Chun also shows (pp. 107–109), that, while many of the Atlantic Siphonophoræ are found in the Mediterranean, there are others which are peculiar to the Mediterranean and have not been seen in the Atlantic; while there are also a number of Atlantic species that do not appear in the Mediterranean. It is possible, as future researches may demonstrate, that there are a few Siphonophoræ that are restricted to the Gulf of Mexico, or the Bahama Banks, but as yet we are certainly not justified in making any such statement.

The Ctenophoræ of the Bahama-Tortugas region are not sufficiently well known, and too little has been discovered concerning their distribution to warrant us in drawing general conclusions in regard to their geographical range. Beroë Clarkii and Bolina vitrea appear to be confined to the West Indies and the southern Atlantic Coast of the United States, while Ocyroë crystallina probably has a wider distribution over the Tropical Atlantic. The so-called "Eucharis multicornis," "Hormiphora plumosa," and "Beroë ovata" of the Tortugas have not been studied with sufficient care to warrant our stating that they are actually identical with the Mediterranean species bearing the same names.

Comparison of the Bahama-Tortugas Fauna with that of the Fiji Islands and Tropical Pacific.

In 1897, A. Agassiz and the author made a study of the Acalephian fauna of the Fiji Islands, South Pacific, in 18° S. Lat., 178° E. Long. from Greenwich. The results of our investigations have been published in the Bulletin of the Museum of Comparative Zoölogy at Harvard College, 1899, and we there show that the Hydromedusæ and Siphonophoræ of the Fiji Islands are very closely related to those of the Tortugas, Florida. All of the Hydromedusæ and Siphonophoræ found by us in the Fiji Islands belong to well-known Atlantic genera. In the case of the Hydromedusæ 4 Fijian species are so closely related to forms found at the Tortugas that we are unable to distinguish any specific difference between them, and therefore we venture to assert that they may be identical species. These forms are Æginella dissonema, Halitiara formosa, Pandea violacea, and Æquorea floridana. It will be observed that only one of these identical species belong to the Trachylina (*i. e.* A. dissonema), the other three being Leptolina forms. In addition to the species already mentioned, the following genera of Hydromedusæ are represented both in the Fiji Islands and in the Tortugas by very closely allied, although distinct species, — Aglaura, Eutima, Laodicea, Oceania, Epenthesis, and Tiaropsis.

Among the Siphonophoræ (Abyla quincunx, Aglaisma quincunx) and Agalma Pourtalesii are found both at the Tortugas and Fiji Islands. Sphæronectes Köllikeri of the Fiji Islands and Tropical Pacific is certainly very closely allied to Sphæronectes gracilis of the Tortugas and Tropical Atlantic; and the two species may eventually prove to be identical, and the same may be said of Nectophysa Wyvellei.

The Scyphomedusæ of the Fiji Islands are with two exceptions quite distinct from those of the Tortugas, for there are a number of characteristic Rhizostomata in the South Pacific that have no near allies in the Atlantic Ocean. We find, however, in the Fiji Islands a variety of Nausithoë punctata that may prove to be specifically identical with the form found at the Tortugas and in the Mediterranean. Another form, Linerges aquila, of Fiji is closely allied to, although distinct from, L. mercurius of the West Indies.

Among the Ctenophoræ of Fiji, Eucharis grandiformis is a species that bears quite a close resemblance to E. multicornis of the Atlantic and Mediterranean, although it is certainly specifically distinct.

We must conclude, then, that the Acalephian fauna of the Fiji Islands is almost as closely related to that of the Tortugas as the latter is to that of the Canaries. It should be borne in mind, however, that the physical conditions in the Fiji Islands are in many respects quite similar to those of the Tortugas, and are very different from those of the Canary Islands. In both the Fiji and Tortugas Islands we find luxuriant coral reefs and wide areas both of deep and shallow water, and in addition the temperature of the water in the two groups of islands is very nearly the same. In the Canaries, however, we find few corals, and no extensive shallow areas, the islands being surrounded by water of great depth. The temperature of the water there is also much lower than at the Fiji and Tortugas Islands.

We have shown that the Tortugas medusæ cannot survive in cold water, for not a single species is to be found upon the coast of New England north of Cape Cod. The Tortugas forms that are now established at the Fiji Islands must therefore have passed from the Atlantic into the Pacific Ocean somewhere within the tropical, or warm, regions of the Earth, and there can be but little doubt that the Tropical Atlantic was at one time in direct connection with the Pacific. Under these circumstances the Great Equatorial Current would pour from the Atlantic into the Pacific, and the pelagic life of the tropical regions of both oceans would become closely related. A fuller discussion of this subject, and of the researches of Hill, 1898 (Bull. Mus. Comp. Zoöl., Vol. 28) upon the geological history of the Isthmus of Panama will be found in our paper upon Fiji Acalephs in 1899.

In view of the close relationship that exists between the Acalephian faunæ of the Fiji and Tortugas Islands, one would be led to expect that the medusæ of the Gulf of Panama and the west coast of Mexico would also display a resemblance to those of the West Indies and Tropical Atlantic; and this is, indeed, the case. Maas, 1897, in his report upon the medusæ of the "Albatross" expedition of 1891, records 18 species of Hydro- and Scypho- medusæ belonging to 15 genera. All but one of the genera (Chiarella) are represented in the Atlantic by well-known species. Five of the Hydromedusæ from the Gulf of Panama and Galapagos Islands are represented in the Atlantic by species so closely related to them that, were they found existing side by side in the same region, they would probably be considered to be varieties one of the other. Thus: —

Stomotoca divisa, Maas	is very closely related to	S. pterophylla, of the Bahamas.
Homœonema typicum, Maas		H. militare, of the Atlantic.
Aglaura prismatica, Maas		A. hemistoma, of the Atlantic.
Liriope rosacea, Eschscholtz		L. cerasiformis, of the Atlantic.
Geryonia hexaphylla, Brandt		G. (Carmerina) hastata, Mediterranean.

The following table will serve to show the wide geographical range of some species of Medusæ found at the Tortugas, Florida. (0) indicates absence; (1) indicates that the species is identical with that found at the Tortugas. For example, (1) found in the column headed "Canary Islands" shows that the Canary species is identical with that found at the Tortugas. (1 ±) indicates the presence of a form that *may* prove to be identical with the Tortugas species. (A) indicates the presence of a closely allied but nevertheless distinct species from that found at the Tortugas.

Name of Species.	Tortugas, Florida, 24° 40′ N. Lat. 82° 53′ W. Long.	Canary Islands, Atlantic Ocean, 28° 30′ N. Lat. 15′ W. Long.	Fiji Islands, South Pacific, 18° S. Lat. 178° E. Long.	Mediterranean Sea.
Hydromedusæ.				
Æginella dissonema	1	1	1	0
Aglaura hemistoma	1	1	1±	1
Halitiara formosa	1	0	1	0
Laodicea ulothrix	1	1	A	0
Pandea violacea	1	0	1	0
Æquorea floridana	1	0	1±	0
Staurodiscus tetrastaurus	1	1	0	0
Tiaropsis heliosa	1	0	A	A
Scyphomedusæ.				
Nausithoë punctata	1	?	1±	1
Siphonophoræ.				
Abyla pentagona	1	1	0	1
Abyla quincunx	1	1	1	0
Agalma Pourtalesii	1	0	1	0
Diphyes bipartita	1	1	0	1
Diphyopsis picta	1	1	0	0
Physalia pelagica	1	1	0	1 ?
Rhizophysa Eysenhardtii	1	1	0	0
Rhizophysa Murrayana	1	1	0	0
Sphæronectes gracilis	1	1	1±	1
Ctenophoræ.				
Eucharis multicornis	1 ?	1	A	1

Morphology of Tortugas Medusæ.

Among the new species described in this paper the following are worthy of special notice: *Pseudoclytia pentata*, a hydromedusa, is normally pentamerous, having 5 radial canals 72° apart, 5 gonads, and 5 lips to the proboscis. This curious species has probably been derived, philogenetically, from a pentamerous sport of some form of Epenthesis, and represents the survival of a discontinuous, meristic variation.

Multioralis ovalis is a new genus of Hydromedusæ in which 4 separate manubria are situated upon a single straight chymiferous canal, which traverses the long diameter of the bell.

Eucheilota paradoxa is the only Leptomedusa known which gives rise to young medusæ by a direct process of budding.

Niobia dendrotentacula is a remarkable form of Hydromedusa in which the tentacles develop into new medusæ and are set free to propagate the species. This is accomplished through a process of growth, budding, and fusion of parts. After all of the tentacles have been cast off, the adult medusa reproduces by a sexual process.

In *Bougainvillia niobe*, Mayer, the medusa buds found upon the proboscis are formed entirely from the ectoderm, the entoderm taking absolutely no share in their construction.

Oceania McCradyi of Brooks, 1888, a hydromedusa that produces hydroid-blastostyles upon its gonads, has been found at the Tortugas.

In *Dysmorphosa dubia*, there appear to be 4 rudimentary gonads? upon the 4 radial canals. If future observations confirm this conjecture, the case will be almost unique among Tubularian medusæ.

Summary of Results.

There is at the Tortugas, Florida, a tropical Medusan fauna, only three species of which are established upon the southern coast of New England; and not one species of which is found upon the New England coast north of Cape Cod.

The Hydromedusæ of the Tortugas are more closely related to those of the Fiji Islands, South Pacific, than they are to those of the Canary Islands, off the Atlantic Coast of Africa.

In comparing the Hydromedusan fauna of the Tortugas with that of the Canaries, we see that the Leptolina forms of the Tortugas are *almost wholly* distinct from those of the Canary Islands. A number of Trachylina forms are, however, common to the two groups of islands.

As was shown by Maas, 1893, these Trachylina forms range widely over the open ocean; and this observation has been confirmed by us during the cruise of the U. S. F. C. S. "Albatross" in the Tropical Pacific, 1899–1900.

The Siphonophoræ of the Tortugas are *very* closely related to those of the Canary Islands. They also display a relationship to those of the Fiji Islands, South Pacific.

The Scyphomedusæ of the Tortugas are, for the most part, distinctly West Indian types, and are not closely related to forms known from the African coast.

33 Hydromedusæ, 3 Siphonophoræ, 1 Hydroid, and 2 Scyphomedusæ are new to science, and 44 forms are new to American waters.

DESCRIPTIONS OF SPECIES.

I. HYDROMEDUSÆ.

DIPURENA, McCrady, 1857.

Dipurena fragilis, nov. sp.

Fig. 41, Plate 17.

Specific Characters. — The bell is 4 mm. in height, and is half egg-shaped. The bell walls are of only moderate thickness. There are 4 long slender tentacles each bearing upon its distal end a single knob-shaped mass of nematocyst cells. A single black ocellus is situated in the ectoderm of the outer surface of each tentacle bulb. The velum is prominent. There are 4 slender straight radial canals, and a narrow ring-canal. The proboscis is about 8 mm. in length, and exhibits two distinct annular swollen regions where the gonads are situated. The entoderm of the proboscis, and of the basal bulbs of the tentacles, is ochre-yellow. The entoderm of the distal nematocyst knobs of the tentacles is slightly orange. Several specimens were found at the Tortugas in June, 1897.

This species differs from Dipurena strangulata of Charleston (see McCrady, Proc. Elliott Soc., 1857, p. 33, Plate 9, Figures 1, 2) in that the tentacles are longer and much more slender; and the color of the entoderm of the proboscis and tentacles is light ochre-yellow instead of rich green and red as in the Charleston species.

Dipurena picta, nov. sp.

Figs. 45, 46, Plate 18.

Specific Characters. — The bell is cylindrical in shape and 3 mm. in height. The bell walls are very thick and of a tough gelatinous consistency. There are 4 slender tentacles that are not quite as long as the bell height. These tentacles bear from 3–5 bulb-shaped nematocystic swellings near their distal ends (see Figure 46). The basal bulbs of the tentacles are large, and each one bears a dark purple ocellus. There are 4 straight radial tubes and a narrow circular tube. The velum is not very well developed. The proboscis is about 5 mm. in length and exhibits two distinct annular swellings that mark the places where the gonads are situated. The entoderm of the proboscis and basal bulbs of the tentacles is of a beautiful custard-yellow. The entoderm of the nettle knobs of the tentacles is port-wine-colored.

Two specimens were found at the Tortugas, Florida, during the first week in August, 1898.

This species is closely allied to Dipurena dolichogaster, of the Mediterranean (see Haeckel, Syst. der Medusen, 1879, p. 25, Taf. II., Figures 1–7). It differs, however, from the Mediterranean form in that the bell is much thicker and more nearly cylindrical in shape, and there are fewer nematocyst-bearing bulbs upon the tentacles.

STEENSTRUPIA, Forbes, 1848.

Steenstrupia gracilis, Brooks.

Figs. 36, 37, Plate 16.

Steenstrupia gracilis, Brooks, W. K., 1882, Studies Biol. Lab. Johns Hopkins Univ., Vol. II. p. 144.

Specific Characters. — The bell is 4.5 mm. in height, and is surmounted by a slender apical projection fully 2 mm. in length. There are 2 rudimentary tentacle bulbs, one short, stiff tentacle, and one long tentacle which is ringed with a number of annular swellings. The velum is well developed. There are 4 slender radial canals and a narrow ring-canal. A long slender canal runs up from the proboscis into the apical projection of the bell. In mature specimens (Figure 36) the proboscis extends a short distance beyond the velar opening. The proboscis is cone-shaped, and the mouth is a simple round opening without oral lappets. The entoderm of the proboscis is intense yellow-green and rose-color. The entoderm of the tentacles is either yellow-green or rose-colored. Found at the Tortugas, Florida, and on the North Carolina coast, in July and August.

DINEMA, Van Beneden, P. J., 1867.

Dinema jeffersoni,[1] nov. sp.

Fig. 126, Plate 37.

Specific Characters. — The bell is dome-shaped and higher than it is broad; the height being about 1 mm. and the breadth 0.75 mm. The outer surface is sparsely sprinkled with nematocyst cells. There are 2 short marginal tentacles and 2 well-developed tentacle bulbs. The tentacles are covered with numerous small, wart-like, nematocyst-bearing swellings. The basal bulbs are well developed. There are 4 ocelli, one in each tentacle bulb. These ocelli are ectodermal and are situated on the centripetal sides of the bulbs. The velum is well developed. There are 4 straight narrow radial canals and a simple slender circular vessel. The proboscis is about as long as the height of the bell cavity. It is simple, round, and tubular, and the mouth-opening is situated at the extremity of a short cylindrical neck. A simple, short-style canal extends upward from the gastric cavity into the gelatinous substance of the bell. The entoderm of the tentacles and tentacle bulbs is of a delicate green. The ocelli are bright red-brown, and the entoderm of the proboscis is flesh-colored. This form is occasionally met with at the Tortugas late in May and early in June.

Dinema floridana, nov. sp.

Specific Characters. — The bell is about 4 mm. in height and 3 mm. in diameter. The gelatinous substance is thin and uniform, and the side walls of the bell are vertical. There are 2 well-developed, radially situated tentacles. Near the distal end of each of these tentacles there is a large knob-shaped swelling which terminates in a thin, nematocyst-bearing lash. The knob-shaped swelling is hollow and is connected with the general gastro-vascular system of the medusa by means of a narrow tube which extends throughout the length of the entodermal core of the tentacle. The basal bulbs are not large and there are no ocelli. In addition to the 2 long tentacles there are 2 simple rudimentary tentacle bulbs 90° from the well-developed tentacles. The velum is well developed. There are 4 straight narrow radial canals. The proboscis is flask-shaped, being narrower at its base than at the middle of its length. It extends a short distance beyond the velar opening, and the mouth is a simple round opening, at the extremity of a long narrow neck. The entoderm of the proboscis and tentacle bulbs is bright yellow. The entoderm of the swollen distal ends of the tentacles is yellow flecked with orange.

A single specimen of this medusa was found at the Tortugas, Florida, June 17, 1897.

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[1] Named after Fort Jefferson, at the Tortugas, Florida.

HALITIARA, Fewkes, 1882.

Halitiara formosa, Fewkes.

Halitiara formosa, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. IX. p. 276, Pl. IV. Fig. 2.

Specific Characters. — The bell is 3 mm. in height, and is provided with a solid apical projection. There are four long, radially situated tentacles, the distal ends of which are usually carried coiled in a tight helix. These tentacles are hollow, and have well-developed basal bulbs. In addition to these there are 24–35 short, solid tentacles that are usually carried tightly coiled. The velum is well developed. There are 4 straight, narrow radial tubes and a narrow, simple, circular vessel. The proboscis is pyriform, and extends for about half the distance from the apex of the bell cavity to the velar opening. The mouth is a simple round opening, and there are no prominent lips. The gonads are situated within the proboscis. In the case of the female the ova are very large and conspicuous. The entoderm of the proboscis and tentacle bulbs in the females is green; in the males, light brown. This medusa is certainly the commonest of all at the Tortugas, Florida, during the summer months. We have found this species in the Fiji Islands.

ECTOPLEURA, Agassiz, L., 1862.

Ectopleura minerva, nov. sp.

Fig. 38, Plate 16; and Fig. 125, Plate 37.

Ectopleura, sp., Fewkes, J. W., 1883, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XI. p. 85, Pl. I. Fig. 11.

This form possesses but two marginal tentacles instead of four, as in all other species of Ectopleura.

Specific Characters. — The bell is 2.5 mm. in height and is pear-shaped, having a well-developed apical projection. The gelatinous substance is of only moderate thickness. 8 rows of nematocyst cells extend from the tentacle bulbs to the bell apex. There are 2 well-developed tentacles, and 2 small tentacle bulbs. There are 6–9 separate, wart-like swellings upon the upper (aboral) side of each tentacle. These swellings are crowded with nettling cells. The velum is well developed. There are 4 straight, narrow, radial canals and a slender circular vessel. The proboscis is pear-shaped and is about $\frac{2}{3}$ as long as the height of the bell cavity. A simple, short style-canal extends upward into the apical projection of the bell. The entoderm of the proboscis and tentacles is of a delicate purple, while the supporting lamella of the bell is of a decided green. There are a large number of brilliant yellow spots in the radial canals and tentacle bulbs. This form is rare at the Tortugas, Florida. It was found by Fewkes, 1883, at the Bermudas.

STOMOTOCA, Agassiz, L., 1862.

Stomotoca australis, nov. sp.

Fig. 2, Plate 1.

Specific Characters. — The bell is about 2.5 mm. in height, and there is a well-developed, solid, conical projection upon the aboral surface of the umbrella. The bell walls are thin. There are 2 large diametrically opposed tentacles, which are situated at the foot of two of the radial canals. The basal bulbs of these tentacles are hollow, and are long and conical. In addition to the two long tentacles there are two rudimentary tentacle bulbs situated at the bases of the radial canals 90° away from the long tentacles. There are 8 ectodermal ocelli. 4 of these are situated upon the centrifugal surfaces of the 4 tentacle bulbs, and the 4 others occupy intermediate positions upon the bell margin. The velum is wide. The radial canals and circular tube are broad, and their edges are smooth and simple. The proboscis is short and urn-shaped, and extends about halfway from the inner apex of the bell cavity to the velar opening. The gonads occupy complexly folded and corrugated regions upon the sides of the stomach. The proboscis and tentacle bulbs are yellow, or greenish yellow. The ocelli are orange. The entodermal core of the proboscis often displays a faint orange tinge. This species is common throughout the summer at the Tortugas, Florida.

Stomotoca rugosa.

Stomotoca apicata, Fewkes, J. W., 1881, Bull. Mus. Comp. Zoöl., Vol. VIII. p. 152, Pl. II. Figs. 1, 4, 9.

Amphinema apicatum, Brooks, W. K., 1883, Stud. Johns Hopkins Biol. Lab., Vol. II. p. 473.

This species has usually been confounded with Stomotoca apicata, L. Agassiz. Stomotoca apicata, L. Agassiz, is, however, distinguished from S. rugosa by the circumstance that the entoderm of the proboscis in the male is green, or straw-colored, and in the female, dull ochre; and the tentacle bulbs in the male are purple, and in the female, dull ochre. In the form described by Fewkes and Brooks, for which we propose the name S. rugosa, the entoderm of the proboscis and of the tentacle bulbs is always brick-red in both sexes.

Specific Characters. — The bell is 5 mm. high and 3 mm. broad. It bears an apical projection which in some individuals is long and slender and in others short and blunt. The substance of this projection is solid throughout. There are 2 long, well-developed tentacles and 14 small rudimentary ones.

The basal bulbs of the long tentacles are large and hollow. When fully stretched, the long tentacles attain a length of 4–10 times the bell height. The velum is well developed. There are 4 broad radial tubes, and also a broad circular vessel with jagged outlines. The proboscis is flask-shaped, the lips being flanged and quite prominent. The mature sexual products are found in the ectoderm of the proximal portion of the proboscis where the outer surface is folded into a complex series of ridges. The bell is transparent. The entoderm of the tentacle bulbs and of the proboscis is brick-red. In some individuals the entoderm of the 4 radial tubes and of the circular vessel exhibits a faint tinge of red. The specimens of this species from the Tortugas, Florida, are peculiar in that the red color of the proboscis and tentacle bulbs is streaked with black. In some cases, after the medusæ had been confined in aquaria for a number of days, the proboscis and tentacle bulbs became wholly black.

This medusa is very common at Newport, Rhode Island, but does not extend north of Cape Cod. It is found all along the southern coast of the United States, but is rare at the Tortugas, Florida.

Hydroid, and young medusa. — Brooks, 1883, describes the hydroid of this species. It is a Perigonimus, very much like P. minutus, Allman (1871; Tubularian Hydroids, p. 324, Plate XI. Figures 4–6). It was found growing upon the lower surface of the shell of Limulus, fastened to the sand tubes of Sabellaria. The stems are simple and unbranched and are about 0.2 mm. in height. The stems are covered for about two thirds of their length by a delicate, closely adherent film of perisarc to which foreign particles become attached. The stomach occupies about one fourth or one fifth of the stem, from which it is separated by a slight constriction. Each polypite possesses ten tentacles, which point alternately backwards and forwards, those pointing forwards being a little longer than the others. The medusæ are attached by very short peduncles to the sides of the stems. When the medusa is set free it is about 0.5 mm. in height, and there is no trace of the apical projection, which develops in the course of about 8 days.

In an abnormal individual of this species found at Newport, Rhode Island, in July, 1892, there were 4 long tentacles, one at the base of each radial canal. This medusa was maintained alive in an aquarium for more than a month. When first found it had but two diametrically opposed tentacles, each at the foot of a radial canal. The other pair of large tentacles developed later, after the first pair had attained their full length. The medusa then possessed 4 long tentacles and 12 small rudimentary tentacle bulbs. This variation is interesting, as it illustrates the close relationship between Stomotoca and Modeeria.

PANDEA, Lesson, 1837.

Pandea violacea, Agassiz and Mayer.

Fig. 1, Plate 1.

Pandea violacea, Agassiz, A., and Mayer, A. G., 1899, Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. XXXII. p. 160.

Specific Characters. — The bell is pear-shaped and 4 mm. in height. The bell walls are only of moderate thickness. There are 32 tentacles, 8 of these are each about 3 times as long as the bell height, and 24 are small and rudimentary. The basal bulbs of the long tentacles are hollow. There are 32 ocelli, one on each tentacle bulb. The velum is well developed. The proboscis is flask-shaped, its proximal portion being distended by the 4 gonads. The lips are simple and cruciform. There are 4 straight radial tubes, and a broad circular vessel. The entoderm of the proboscis and tentacle bulbs is of a delicate pink. A green streak runs along the outer surface of the entodermal lining of the radial canals. The ocelli are purple in color. The medusa is common at the Tortugas, Florida, throughout the summer. We have found a species at the Fiji Islands that appears to be identical with the Tortugas form. Our figure is drawn from a specimen found at the Tortugas.

TIARA, Lesson, 1843.

Tiara superba, nov. sp.

Fig. 39, Plate 16.

Specific Characters. — The bell is 5 mm. in height and possesses a small apical projection. There are 4 long hollow tentacles and 12 small rudimentary tentacles. A brilliant red eye-spot is found in the ectoderm of the outer surface of each tentacle bulb. The velum is well developed. There are 4 broad straight-edged radial tubes and a broad circular vessel. The proboscis is very broad and the lips are surrounded by complexly fimbricated lappets. The gonads are found in 4 sharply folded, radially arranged regions in the upper portion of the proboscis. The proboscis is bound to the radial tubes by means of 4 mesenteries. The entire gelatinous substance of the medusa is of a delicate rose-pink. The entoderm of the proboscis and tentacles is of a rich rose-color, and the entodermal core of the proboscis is emerald-green. This medusa makes its appearance in June and continues to be common throughout the summer at the Tortugas, Florida.

GEMMARIA, McCrady, 1857.

Gemmaria dichotoma, nov. sp.

Fig. 40, Plate 17.

Specific Characters. — The bell is 3 mm. in height and there is a solid mitre-shaped apical projection. The bell walls are thin. There are two rudimentary tentacle bulbs and two well-developed tentacles. The entodermal core of these large tentacles is hollow. They terminate in a bulb-shaped nematocyst swelling, which in some individuals is provided with delicate bristles. A number of tentaculæ arise from the upper or "dorsal" side of the tentacle, and each one of these terminates in a bulb-shaped swelling similar to that at the distal end of the main tentacle. The youngest and least-developed of these side branches is always found nearest the bell. The basal bulbs of the tentacles are large, and there is a single deep red ocellus in the outer surface of the ectoderm of each. The velum is quite well developed. There are 4 straight radial canals and a narrow circular canal. The proboscis is pyriform and extends about half the distance from the apex of the bell cavity to the velar opening. The entoderm of the proboscis and tentacles is ochre-yellow. Several specimens were found at the Tortugas early in July.

Gemmaria gemmosa, McCrady.

Figs. 137, 138, Plate 41.

Gemmaria gemmosa, McCrady, J., 1857, Gymn. Charleston Harbor, p. 49.
Zanclea gemmosa, McCrady, J., 1857, Gymn. Charleston Harbor, p. 48, Pl. 8, Figs. 4, 5.

Specific Characters. — Hydroid stock; Gemmaria gemmosa. The hydroid was found at the Tortugas, Florida, growing upon a piece of floating gulf-weed (Sargassum). The hydrorhiza is creeping and net-like, and gives rise at irregular intervals to short, more or less twisted hydrocauli. Both the hydrorhiza and hydrocauli are covered with a horny, chitinous perisarc, which in the hydrocaulus displays a number of annulations. The hydrocaulus is corrugated, and opaque in color, throughout its length; and in this respect differs from the European G. implexa described by Allman (1871, Tubularian Hydroids, p. 290, Plate VII.). The fully developed hydranths are only 1.5 mm. in height. They are elongate, and the diameter near the proximal end is a little greater than at the free oral extremity. The tentacles arise in 5–8 whorls from the side of the hydranth. Each whorl contains 4–6 short tentacles. Each tentacle terminates in a distal knob which is armed with a dense cluster of nematocysts. The cells of the shafts of the tentacles are vacuolated, and the tentacles themselves quite stiff and inflexible. 4–8 medusa-buds arise from the side of the hydranth immediately below the proximal whorl of tentacles.

When set free the young medusa possesses 2 well-developed diametrically opposed tentacles and 2 rudimentary tentacle bulbs (Figure 137). The 4 radial, nematocyst-bearing swellings upon the ex-umbrella extend halfway up the sides of the bell from the margin toward the apex. The bell walls are uniform, and very thin and flexible. There are 4 slender radial canals, and the proboscis is a short simple tube with no trace of gonads. Before being set free, the tentacles are carried coiled inward so that they lie protected within the bell cavity. Soon after liberation, however, the tentacles are turned outward. (Compare Figures 137 and 138.) The deep-lying entoderm of the hydranth is of a delicate creamy pink, while the more superficial entoderm is of a translucent milky color. The entodermal cells of the superficial entoderm are large and vacuolated. The hydrorhiza is of a horny yellow color. This species is quite different from Gemmaria implexa of Allman. It is probably the hydroid of Zanclea gemmosa, McCrady, of Charleston Harbor, but not having been able to raise the medusæ we must remain in some doubt concerning its identity.

NIOBIA, nov. gen.

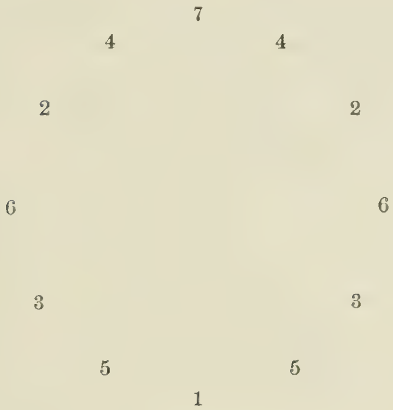
Niobia dendrotentacula, nov. sp.

Figs. 141-143, Plate 42; Fig. 144, Plate 43.

Generic Characters. — Niobia. Cladonemidæ with 2 simple and 2 bifurcated radial canals. There are 4 simple lips to the proboscis, but no oral tentacles. The marginal tentacles develop into free-swimming medusæ.

There is no place in the system of Haeckel (1879; p. 101) for this genus. It cannot be placed among the Dendronemidæ, for it has no oral tentacles, and as it has branched radial canals it cannot be classed among the Pteronemidæ. It combines the essential characters of both of these subfamilies, however, and forms a good connecting link between them.

Specific Characters. — Adult medusa. The bell is slightly flatter than a hemisphere, and is about 4 mm. in diameter. The gelatinous substance is quite thin and uniform, but not very flexible. The tentacles are arranged in bilateral symmetry, the axis being in the diameter of the two simple radial canals (see Figure 144, Plate 43). The oldest tentacle is situated at one end, and the youngest at the other end of this axis. (Figures 142, 144.) Each half of the medusa is a reflection of the other, and the order in age of the tentacles is given by the following diagram, the oldest tentacle being numbered (1) and the youngest (7): —



Tentacles (1) and (7) are situated at the bases of the simple radial canals, while tentacles (2, 2) and (3, 3) are found at the bases of the two bifurcate canals. In addition to these there are the intermediate sets of tentacles (4, 4), (5, 5), and (6, 6); and thus the medusa possesses 12 tentacles, each successive pair being 30° apart. It is very remarkable that through a peculiar process of growth each tentacle bulb is developed into a young medusa which resembles the adult, and is finally set free into the water. Various stages of this process will be seen by an inspection of Figures 141, 142, and 144. The oldest tentacle is the first to be transformed into a new medusa, and the others follow in the order of their age until all of the tentacles have been cast off. The first stage in this process is the development of a hernia-like outgrowth, involving both entoderm and ectoderm, adjacent to and on the centripetal side of each tentacle bulb upon the floor of the sub-umbrella. Soon after this two pointed outgrowths appear on both sides of each tentacle bulb, and finally develop into new tentacles. These outgrowing tentacles become larger, and soon a still younger pair make their appearance centrifugal to the first, and these are soon followed by two others which lie centripetally from the oldest pair. Before this, however, 4 short canals (the radial canals of the future medusa) develop, and place the gastric cavity of the future proboscis into communication with the circular vessel. An opening then appears in the velum of the adult medusa immediately below the proboscis of the future medusa, and this constitutes the velar opening of the new animal. The proboscis becomes cruciform in cross-section, and finally the new medusa is constricted off and becomes free in the condition represented in Figure 142. Here we see that the simple radial canals, the circular canal, the velum, and the oldest tentacle are stolen directly, so to speak, from the parent medusa. The forked canals, proboscis, and younger tentacles are new growths. Even before the outgrowing medusa is detached from the old one, hernia-like outgrowths appear upon the sub-umbrella wall near the bases of *its* tentacles, and thus the process of forming new medusæ is repeated in the next generation. The medusæ are very hardy when detached and grow rapidly, and proceed at once to develop new medusæ from their own tentacle bulbs. When detached, the bell of the new medusa is about 1.5 mm. in diameter. It is difficult to comprehend the philogenetic history of this curious and fortuitous combination of local growth, fusion, and budding which results finally in the formation of a medusa exactly resembling the adult. It is probable, however, that it has been derived from the usual budding process so common in hydromedusæ, but that in this case a greater and greater number of parts have been taken directly from the adult medusa, until the present state has been arrived at. After the original tentacles have been cast off, new ones grow out in their places, and thus the old medusa always has 12 tentacles. After every one of the original 12 tentacles has been cast off, however, the process of forming new medusæ becomes less active and finally ceases altogether. Then the gonads develop in 4 separate interradial regions on the wall of the gastric part of the proboscis. In the female the ova become very prominent, and are finally dehisced into the water. I was unable to raise them, however, and know nothing of the development of the sexual generation. The proboscis is flask-shaped, and there are 4 simple cruciform lips. The entoderm of the proboscis tentacle bulbs and circular canal is ochre-yellow, all other parts of the medusa being transparent. The medusa is very active and thrives well in confinement. Large numbers of them appeared at the Tortugas, Florida, on May 21, and continued more or less common until June 4, 1899.

TURRITOPSIS, McCrady, 1857.

Turritopsis nutricula, McCrady.

Turritopsis nutricula, McCrady, J., 1857, Gymn. Charleston Harbor, p. 25, Pls. IV., V., VIII. Fig. 1.

Modeeria multitentacula, Fewkes, J. W., 1881, Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. VIII. p. 149, Pl. III. Figs. 7–9.

This medusa was well described by McCrady in 1856 and 1857. Fewkes, 1881, however, redescribed it as a new species under the name "Modeeria multitentacula." To add to the confusion respecting this species, a medusa that has since been identified by Martha Bunting, 1894, as Podocoryne carnea, was described by A. Agassiz, 1862, 1865, under the name of "Turritopsis nutricula." The latter author was deceived by the close resemblance of the young of Podocoryne carnea to the young medusa of T. nutricula, McCrady, 1857, into the belief that the two were identical. The mature medusæ, however, are easily distinguished one from the other, and the hydroid stocks differ widely from each other.

Specific Characters. — Mature medusa. The bell is pear-shaped with thin walls, and is 4 mm. in height. There are 40–50 marginal tentacles that are capable of much contraction and extension. There is a single brown, ectodermal, pigment spot upon the centripetal side of each tentacle near the point of its junction with the tentacle bulb. The velum is well developed. There are 4 straight, narrow, radial canals. The proboscis is wide and fills about half of the cavity of the bell. The upper portion of the proboscis consists of highly vacuolated cells, or chambers, through the midst of which run the 4 radial canals. The mouth opening of the proboscis is found at the end of a short, narrow, cylindrical neck, and is surrounded by 4 radially arranged nematocyst-bearing knobs. The gonads are situated within the proboscis. The entoderm of the proboscis is dull yellow, streaked with brownish orange. The ocelli of the tentacle bulbs are orange, or brown in color.

This medusa is extremely abundant from the coast of Cuba to Newport, Rhode Island. It is not found north of Cape Cod, Massachusetts. It is very common in Charleston Harbor, South Carolina, where it is infested by the young of Cunoctantha octonaria. This medusa is one of the few that appears to develop from the hydroid stock both at the Tortugas and at Newport, Rhode Island. For while medusæ indigenous to the Tortugas are often driven into Newport Harbor by southerly winds, very few of these southern visitors establish themselves permanently in the northern waters.

The hydroid stock of this species was found by Brooks, 1886, at Morehead City, North Carolina. It is a Tubularian belonging to the genus Dendroclava. Brooks gives a number of good figures of it in his paper in the Memoirs of the Boston Society of Natural History, Vol. III., 1886.

CYTAEIS, ESCHSCHOLTZ, 1829.

Cytaeis gracilis, nov. sp.

Figs. 122-124, Plate 36.

Specific Characters. — Mature medusa; Figure 122. The bell is dome-shaped and a little broader than it is high, and the aboral apex terminates in a slight projection. The animal is 3 mm. in diameter. The gelatinous substance of the bell is of only moderate thickness. There are 8 quite stiff curled tentacles; 4 radial and 4 interradial. The radial tentacles are about two thirds as long as the bell height, while the interradial ones attain only about one half this length. The basal bulbs of all of the tentacles are large and deeply pigmented. The velum is broad. There are 4 straight, narrow, radial canals, and a simple slender circular vessel. The proboscis is mounted upon a short, wide peduncle. The gastric portion of the proboscis is only about one half as long as the height of the bell cavity. The mouth is a simple, round opening, surrounded by 8 unbranched oral tentacles. 4 of these tentacles are radial and 4 interradial in position, and each one terminates in a knob-like end formed of spindle-shaped nematocyst cells. Medusa buds arise from the sides of the gastric portion of the proboscis. When set free each medusa possesses 4 short equally developed tentacles. The entoderm of the proboscis is usually red in color, although sometimes the inner core is red or pink and the outer annulus is green. Each tentacle bulb is provided with a dense mass of red entodermal pigment, which in the case of the radial tentacles extends for a considerable distance up the course of the radial canals.

Young Medusæ. — The youngest medusa found free in the water was 1.5 mm. in height (Figure 124), and the bell was about twice as high as it was broad. The gelatinous substance was quite thin. There were only 4 marginal tentacles and these were radial in position. The distal tips of these tentacles were slightly knobbed and their entoderm was tinged with green. There were 8 simple oral tentacles, and the proboscis lacked a peduncle. In an older individual, which was 2.5 mm. in height, the bell was pyriform. The proboscis possessed a peduncle, and there were 8 marginal tentacles, 4 radial and 4 interradial. There were no traces of medusa buds upon the proboscis.

This medusa was quite common at the Tortugas, Florida, about the middle of June, 1899.

DYSMORPHOSA, PHILIPPI, 1842.

Dysmorphosa dubia, nov. sp.

Figs. 64-66, Plate 22.

Specific Characters. — The bell is egg-shaped and 1.5 mm. in height. The bell walls are thin and flexible. There are 8 quite stiff tentacles (Figure 66) that are carried curled slightly upward. The distal ends of these tentacles are thickly covered with nettling cells. A very large black ocellus is situated in the ectoderm of the under side of each tentacle bulb. The velum is well developed. There are 4 straight, narrow, radial tubes; and a slender circular canal. The proboscis is pear-shaped, and there is a slightly developed peduncle. 4 radially situated oral tentaculæ surround the mouth. Each one of these terminates in a knob-like cluster of nematocysts (Figure 65). 4 small, rudimentary gonads ? appear to be developed at points midway along the lengths of the 4 radial canals. The entoderm of the proboscis, tentacle bulbs, and gonads ? is of a delicate yellow. One specimen was found at the Tortugas, Florida, on July 20, 1898.

The presence of what appear to be gonads ? upon the radial tubes is certainly remarkable; it should be remembered, however, that such appearances are not unknown among genera of Tubularian medusæ that normally bear their gonads upon the proboscis. In the case of Dipurena halterata bodies that are very similar in general appearance to rudimentary gonads are found upon the radial canals. (See Forbes, E., 1848, British Naked-Eyed Medusæ, p. 53, Plate VI., Figures 1, b, c, d. Also Browne, E. T., 1898, Proc. Zoöl. Soc. London, p. 816, Plate 49, Figure 2.)

Dysmorphosa minuta, nov. sp.

Fig. 42, Plate 18.

Specific Characters. — The medusa is extremely minute, the bell being only 0.3 mm. in height. It is pear-shaped and the walls are quite thick. The gelatinous substance is remarkably delicate, and the medusa soon contracts into a shapeless mass in captivity. There are 8 marginal tentacles, with well-developed basal bulbs. The velum is small. There are 4 straight, slender radial canals and a narrow circular vessel. The proboscis possesses a distinct peduncle. The gastric portion as well as the peduncle is 4-sided in cross-section. 4 well-developed oral tentacles surround the mouth, one being situated at each radial corner. Each of these tentacles terminates in a knob-shaped distal end, which is thickly covered with nematocysts. The entodermal cells of the oral tentacles are disk-shaped and highly vacuolated. Several medusa buds in various stages of development are found upon the upper interradial regions of the gastric portion of the proboscis. In some specimens the entoderm of the proboscis and tentacle bulbs is turquoise blue, and in others lilac. The medusa was common at the Tortugas, Florida, in the middle of July, 1898. It is the smallest hydromedusa known. Its color is also very different from D. fulgurans, A. Agassiz, of Newport Harbor.

BOUGAINVILLIA, Lesson, 1836.

Bougainvillia frondosa, nov. sp.

Fig. 5, Plate 3.

Specific Characters. — The bell is dome-shaped and about 2 mm. in height. There are 4 bunches of marginal tentacles, which are situated at the bases of the 4 radial canals. Each tentacle bulb gives rise to but 2 tentacles, thus making 8 in all. There are no ocelli at the bases of the tentacles. The velum is small. There are 4 straight, simple, radial tubes. The proboscis is short, thick, and flask-shaped, and extends only about one half of the distance from the inner apex of the bell cavity to the velar opening. There are 4 radially situated oral tentacles, each of which branches dichotomously two or three times. The mature gonads are found in 4 radially situated swollen regions upon the ectoderm of the proboscis, above the origins of the oral tentacles. There are a number of flask-shaped bodies with narrow necks protruding from the surface of the proboscis in the region of the gonads. Each of these flask-shaped capsules is filled with yellow-colored cells. Although it is possible that these may be developing planulæ, we incline to the opinion that they are parasitic zoöxanthellæ. We are led to this opinion on account of the decided yellow-green color of these cells, and also because we have found similar capsules scattered irregularly over the surface of the sub-umbrella of Laodicea ulothrix at the Tortugas. The entoderm of the proboscis and tentacle bulbs is cream-colored, and the tips of the tentacles are turquoise. A single specimen of this medusa was found at the Tortugas, Florida, on June 11, 1897, and another in June, 1899.

Bougainvillia niobe, Mayer.

Bougainvillia niobe, Mayer, A. G., 1894, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXV. p. 236, Pl. I. Fig. 2.

Specific Characters. — The bell is 6.75 mm. in height and 4.8 mm. broad. The bell walls are thick and gelatinous. The marginal tentacles arise from 4 radially situated bulbous swellings, each one of which gives rise to 6–8 tentacles. At the base of each tentacle, upon the inner or centripetal side, there is a dark-colored pigment spot, or ocellus. This is an ectodermal structure, and it projects slightly from the surface of the tentacle. The tentacles are not very flexible and are about as long as the bell height. The velum is well developed. There are 4 straight, narrow, radial tubes. The proboscis is wide, but not very long, extending only about half the distance from the apex of the bell cavity to the velar opening. There is a small peduncle. There are 4 large, radially arranged bunches of oral tentacles. These arise as 4 main stems, each of which branches dichotomously 4 times, thus giving rise to 16 tentacle tips from each quadrant of the proboscis. These terminal tentacle tips are slightly knobbed, and are composed chiefly of nematocyst cells. The tentacles of the proboscis are very flexible and may be observed waving gracefully to and fro within the cavity of the bell.

The most remarkable characteristic of this species is the presence of numerous medusa buds that arise from the gastric region of the proboscis. These budding medusæ are found in 8 radially arranged clusters situated near to and on both sides of the places where the 4 radial tubes enter the gastric portion of the proboscis. A study of sections of the proboscis of medusæ killed in Flemming's Chrome-Osmic-Acetic, and stained in Kleinenberg's 70% Alcoholic Hæmatoxylin, has shown that *the proliferating medusæ are formed entirely from the ectoderm*, the entoderm taking no part whatsoever in their formation. There is a very well-defined lamella between the ectoderm and the entoderm of the proboscis of the parent medusa, and the membrane of this lamella is never broken during the time of the formation of the medusa bud from the ectoderm of the proboscis. Indeed, the gastro-vascular cavity of the budding medusa is never connected with that of the parent. The medusa buds develop very much as has been demonstrated by Chun (1895; Bibliotheca Zoologica, Heft 19, Lfg. 1, p. 1–51, Taf. I., II.) in Rathkea octopunctata, and Lizzia Claperèdei; excepting that while in the forms studied by Chun the gastro-vascular cavity of the bud finally acquires a connection with that of the parent, in Bougainvillia niobe no such connection is ever formed. Chun concluded that medusa buds which are derived entirely from ectoderm cannot be homologous with those that are formed from both ectoderm and entoderm in the manner commonly observed in Hydroids, and in the medusa of Sarsia; for it is necessary, if organs be homologous, that they have a similar origin. It has occurred to us, however, that Chun may be mistaken in this conclusion, and that his statement may be more a matter of definition than of fact; for it may well be that, in the course of phylogeny, the entoderm has come to take less and less part in the formation of medusa buds, until finally, as in the case of Bougainvillia niobe, it has abandoned all share in their formation. Considered from the physiological standpoint it may be that in B. niobe the ectoderm of the parent proboscis being very thick, there is an abundance of cells from which to form the bud without having resource to those of the deep-lying and somewhat inaccessible entoderm. When set free the young medusa possesses 4 radial tentacles. The bell of the medusa is transparent, and the entoderm of the proboscis and tentacle bulbs is rosin-yellow.

Found in Nassau Harbor, New Providence Island, Bahamas, in March, 1893.

It is interesting to notice that Hartlaub (1897; Hydromedusen Helgolands) has shown that the sex cells of Bougainvillia superciliaris are first found in the entoderm of the young medusa, and that as development proceeds they pass into the ectoderm, where they become mature. It is possible that the cells which give rise to the medusa buds of Bougainvillia niobe are similarly derived from the entoderm of the young medusa. We have not seen the young and immature medusa of B. niobe, and in the mature animal the supporting lamella between the ectoderm and entoderm of the proboscis is very distinct and unbroken, and we have never succeeded in discovering any cells which were passing through it.

Margelis carolinensis, Agassiz, L.

Hippocrene carolinensis, McCrady, J., 1857, Gymn. Charleston Harbor, p. 62, Pl. 10, Figs. 8–10.

Margelis carolinensis, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 344.

In the Tortugas and Charleston Harbor examples of this species, the entoderm of the tentacle bulbs and of the proboscis is of a delicate sage-green color; while the gonads are cream-colored, and the tentacular ocelli dark-brown or black. In northern examples of this medusa, found at Newport, Rhode Island, and Naushon, Massachusetts, A. Agassiz describes the color of the tentacle bulbs as brilliant red surrounded by a green edge bordered with light yellow; and the digestive cavity as brick-red, or green. No such brilliant coloration has been seen in the southern specimens. The medusa is not very common at the Tortugas, being met with only occasionally during the summer months. In Charleston Harbor, South Carolina, however, it is extremely abundant.

LIZZIA, Forbes, 1846.

Lizzia elegans, nov. sp.

Fig. 127, Plate 38.

Specific Characters. — The bell is 3–7 mm. in height, and the gelatinous substance is of moderate and nearly uniform thickness. The sides of the bell are almost straight and vertical, and the top is dome-shaped. There are eight groups of marginal tentacles, 4 radial and 4 interradial. Each radial group is composed of 4, and each interradial of 3 tentacles. The tentacles are quite stiff and curve upward, and are only about one-half as long as the bell height. There is a small dark-brown ectodermal ocellus upon the under (oral) side of each tentacle near the basal bulb. The velum is wide and provided with strong muscles. There are 4 straight, narrow, radial canals, and a simple circular vessel. There is a well-developed conical peduncle to the proboscis, down which the radial canals lead in their course to the gastric sac. The gastric part of the proboscis is cruciform in cross-section and pear-shaped in general longitudinal contour. The mouth is a simple round opening without prominent lips. The oral tentacles arise from the four radial sides of the proboscis at a short distance above the mouth. Each tentacle branches dichotomously 3 times and then each tip terminates in three small branches which are covered with nematocysts. The entodermal cells of the oral tentacles are chordate. The genital products are situated upon the 4 radial sides of the gastric portion of the proboscis. The entoderm of the tentacle bulbs and radial canals is of an intense opaque pearly-white color, often displaying a tinge of pink. The entoderm of the gastric portion of the proboscis is of an intense green, and the oral tentacles are pearly-pink. The intense opaque color of the radial canals contrasting with the hyaline transparency of the bell renders this medusa one of the most beautiful to be found at the Tortugas, Florida.

Several specimens were captured early in July, 1899.

DISSONEMA, Haeckel, 1879.

Dissonema turrida, nov. sp.

Figs. 3, 4, Plate 2.

Specific Characters. — Adult medusa ; Figure 3. The bell is about 4 mm. in height. It is blunt and cone-shaped, and there is a prominent apical projection, which is hollow. There are 2 large hollow tentacles, which when expanded are 3–4 times as long as the bell height. In addition to these, there are 14 small solid tentacles, or marginal cirri. There are 16 ocelli, one at the base of each tentacle. These ocelli are situated within the ectoderm of the outer (centrifugal) side of the tentacles. The proboscis is pyriform, and the lips project beyond the velar opening. The walls of the proboscis are very thin, and the lips are crenulated. The 4 radial canals are broad, and the 4 gonads occupy their proximal halves. In the female each gonad contains about six large ova, which stand out prominently over the surface of the organ. The entoderm of the proboscis and tentacles is of a delicate shade of green. The genital organs and circular canal are tinged with pink.

Young Medusa. — Figure 4, Plate **2**, represents a young medusa of this species in which the genital organs have not yet made their appearance. There are but 4 tentacles, and 8 ocelli; and it is remarkable that the long tentacles are as yet solid, although they become hollow throughout their length in the adult medusa. This species is common throughout the summer at the Tortugas, Florida.

NETOCERTOIDES, nov. gen.

Netocertoides brachiatum, nov. sp.

Figs. 43, 44, Plate 18.

Generic Characters. — Cannotidæ with 8 bifurcating, radial canals. 16 canals reach the circular vessel. There are neither marginal sense-organs nor cirri.

Specific Characters. — The bell is mitre-shaped and 3 mm. in height. There are 32 marginal tentacles. 16 of these are well developed, and are situated at the bases of the 16 radial canals; and the others are smaller, and alternate with the large tentacles in position. The large tentacles are only about one quarter as long as the bell height, and the others are much smaller. There are no marginal sense-organs. The velum is well developed. The proboscis has the shape of an 8-rayed star, each ray of which bifurcates, thus giving rise to 16 radial canals which reach the circular vessel. The gastric portion of the proboscis is wide, but flat, and the mouth extends but a short distance down into the bell cavity. The gonads appear to be situated upon the 8 rays of the stomach. Two specimens were found at the Tortugas, Florida, on July 10, 1898.

As it floats in the water this medusa bears a wonderfully close resemblance to the little pelagic Alga (Trichodesmium), which is very abundant at the Tortugas.

STAURODISCUS, Haeckel, 1879.

Staurodiscus tetrastaurus, Haeckel.

Figs. 47-49, Plates 18, 19.

Staurodiscus tetrastaurus, Haeckel, E., 1879, Syst. der Medusen, p. 145, Taf. IX. Figs. 1–3.

Specific Characters. — The bell is 4.5 mm. in diameter, and about twice as wide as it is high. In adult medusæ there are 8 long flexible tentacles with hollow basal bulbs. In some specimens there are 24, and in others 16 sensory clubs upon the bell margin. There are always 32 black entodermal ocelli, one at the base of each tentacle bulb and sensory club. The velum is well developed. Only 4 radial canals reach the circular vessel. Each of these canals gives rise to a pair of side branches that end blindly. The gonads are situated upon these side branches and upon the distal portion of each radial canal. The proboscis bears 4 prominent lips. The color of the entoderm of this medusa is green or yellow.

In the youngest specimen observed, the bell was 1 mm. in diameter and about as high as it was broad. There were 4 well-developed tentacles, 4 rudimentary tentacle bulbs, and 8 marginal clubs (see Figure 47, Plate **18**). The medusa was very common at the Tortugas, Florida, in July and August, 1898. Haeckel, 1879, found this species in the Canary Islands, at Lanzerote.

TETRACANNOTA, nov. gen.

Tetracannota collapsa, nov. sp.

Figs. 14-16, Plates 7, 8.

Generic Characters. — Tetracannota is closely allied to Cannota and Berenice. It may be defined as having 16 radial canals, which in the adult become arranged in 4 groups, each group consisting of 4 canals. Gonads 16 in number, and situated upon the distal regions of the radial canals. An entodermal pigment spot at the base of each tentacle. No otocysts. Tentacles numerous.

Specific Characters. — Adult medusa; Figure 14. The bell is 7 mm. in diameter, and about as high as it is broad. The top is dome-shaped, and the side walls are vertical. There are 16 well-developed tentacles that are carried tightly coiled in close helices. In addition to these there are 112 very small, rudimentary tentacles. Dark-brown entodermal pigment is found at the base of each tentacle. There are 16 radial canals, arranged in 4 groups of 4 each. The gonads are found in the proximal portions of the 16 radial canals very near to the point where they branch off from the proboscis. The peduncle of the proboscis is wide and prominent. The proboscis possesses 8 slightly crenulated lips. The entoderm of the proboscis in some specimens is green, in others pearly-white or yellowish. The entodermal pigment spots at the bases of the tentacles are dark brown.

Stages in Development. — The youngest medusa observed possessed a bell 1.5 mm. in diameter (see Figure 15). It had 4 simple radial canals, and 32 tentacles, 4 well developed and 28 rudimentary. The velum was prominent. There were 4 lips to the proboscis, and as yet no peduncle. There was no trace of the genital organs. In the next older stage (Figure 16), we find 16 radial canals, and 8 lips to the proboscis. As yet there is no peduncle and no trace of the gonads, nor have the radial tubes grouped themselves into four bundles as in the adult.

This medusa was very common at the Tortugas in June, and ample opportunity for observing its transformation was afforded. It possesses the curious habit of collapsing into an almost shapeless mass, in which condition it may remain for several hours and then "straighten out" and swim about in excellent condition.

Fewkes, 1883 ("On a Few Medusæ from the Bermudas," Bull. Mus. Comp. Zoöl., Vol. XI., No. 3, Figures 7, 7ª) has evidently figured the young of this species under the name of "Larva of an unknown Tubularian."

DYSCANNOTA, Haeckel, 1879.

Dyscannota gemmifera.

Fig. 17, Plate 8.

Willia ornata? Brooks, W. K., 1880, American Naturalist, Vol. XIV. p. 670.

Willia ornata, Brooks, W. K., 1881, Studies Johns Hopkins Univ. Marine Lab., Vol. II. p. 144.

Willia gemmifera, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. IX. p. 300, Fig. 24, Pl. I.

Specific Characters. — The bell is hemispherical, with a slight apical projection, and is 4 mm. in diameter. There are 12 long tentacles with well-developed basal bulbs. Each tentacle arises from the point of juncture of a radial tube with the circular vessel. The velum is well developed. 4 radial vessels arise from the proboscis, and each of these gives rise to two side branches, so that 12 radial tubes reach the circular vessel. In addition to these 12, very slender tubes branch off at right angles to the circular vessel and end blindly in the gelatinous substance of the bell. These tubes alternate with the 12 radial tubes and tentacles. Each one terminates under a cluster of nematocysts upon the outer surface of the bell. The proboscis is long and slender, and reaches about three quarters of the distance from the apex of the bell cavity to the velar opening. It is provided with 4 slightly recurved and fimbricated lips. This species is remarkable in that a stolon arises from each of the 4 main radial canals near to their point of juncture with the proboscis. Each of these stolons gives rise to a number of medusa buds. The medusæ become free and thus the species is perpetuated. The proboscis is of a decided sage-green, and the entoderm of the basal bulbs of the tentacles is brown. A number of specimens of this medusa were found at the Tortugas, Florida, in June. A single specimen was found by Brooks at Beaufort, North Carolina. Brooks considered it to be an asexual form of Willetta ornata, and this explanation may prove to be correct; we have not found the sexual form of W. ornata, however, at the Tortugas, and incline to regard it as a distinct species.

The species differs from the common Willia ornata, A. Agassiz, of Buzzard's Bay and Newport Harbor, in that the proboscis is far more slender, the narrow tubes branching off from the circular vessel end each in a single cluster of nematocysts, instead of several clusters as in Willetta ornata; and above all, the possession of stolons bearing medusa buds separates this form from all other known Atlantic species of Willetta. It is interesting to notice that Huxley (1891, Anatomy Invert. Anim., p. 120, Figure 17) took a species of Willsia (Willetta) in the north Pacific, in which medusa-bearing stolons were developed at the point of bifurcation of each of the four main radial canals.

LAODICEA, Lesson, 1843.

Laodicea neptuna, nov. sp.

Figs. 50-52, Plate 20.

Specific Characters.— The bell is a little more than a hemisphere, and is 2.5 mm. in diameter. There are 8 short tentacles with large basal bulbs, and 8 small rudimentary tentacle bulbs. The tentacles are thickly covered with nematocysts and are usually carried coiled in a contracted bunch. A single, large, black ocellus is found at the base of each tentacle. There are numerous small nematocyst-bearing cirri upon the bell margin between the tentacles. The velum is well developed. There are four straight radial tubes, the upper regions of which, adjacent to the proboscis, are occupied by the gonads. The proboscis reaches slightly beyond the velar opening, and the lips are surrounded by 4 prominent clusters of nematocyst cells. The color of the entoderm of the proboscis, tentacle bulbs, and circular and radial tubes is pearly-white. The entodermal lamella of the bell is of a delicate shade of green. This medusa was occasionally found at the Tortugas, Florida, during July and August, 1898.

Laodicea ulothrix, Haeckel.

Laodicea ulothrix, Haeckel, E., 1879, Syst. der Medusen, p. 133, Taf. VIII., Figs. 5–7.

Specific Characters. — The bell is about 20 mm. in diameter and is about twice as broad as it is high. (Haeckel, 1879, p. 133, says "etwa doppelt so hoch als breit.") This is doubtless a misprint. There are 70–100 long, slender, stiff tentacles, the distal ends of which are coiled in a close helix. The basal bulbs of these tentacles are large and hollow, and there is a well-developed ectodermal ocellus upon the inner (centripetal) side of each bulb. In addition to these ocelli one often sees small spur-like projections upon the outer (centrifugal) sides of the tentacle bulbs. Not all of the tentacles possess these spurs. Sensory clubs and cirri are scattered somewhat irregularly between the tentacles. The sensory clubs are almost as numerous as the tentacles. They are flask-shaped, and their entodermal cores are in direct connection with the entoderm of the circular tube. There are no otoliths. The cirri are usually less numerous than the tentacles. They are coiled in a helix, and their distal ends are covered with large spindle-shaped nematocyst-capsules. The velum is well developed. There are 4 straight, narrow, radial tubes, the proximal halves of which, adjacent to the proboscis, are occupied by the gonads. The proboscis is short, and there are 4 recurved lips. The entoderm of the proboscis, gonads, and tentacle bulbs is brownish-white, or greenish-white in color. This medusa is one of the commonest at the Tortugas, Florida. Haeckel found it at the Canaries, and Brooks describes it from the Bahama Islands. The distribution of the sensory clubs is usually more irregular than is described by Brooks.

TIAROPSIS, Agassiz, L., 1849.

Tiaropsis punctata, nov. sp.

Figs. 60-63, Plate 22.

Tiaropsis diademata, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl., Vol. IX. p. 277, Pl. VII. Figs. 13–14.

Specific Characters. — The bell is bluntly cone-shaped and is 4 mm. in diameter. There are 4 well-developed, radially placed tentacles, the distal ends of which are usually coiled in a close helix. In addition to these there are 4 rudimentary tentacle bulbs. The 8 marginal sense-organs are situated midway between the 8 tentacles. Each of these organs consists of a pocket-like fold of the velum containing 8–13 otoliths. Immediately above the otocyst there is a well-developed, deeply pigmented eye (see Linko, A., 1899; Travaux Soc. Imp.

des Nat. de St. Pétersbourg, T. XXIX. p. 155, Plate I. Figure 5). The velum is very well developed. There are 4 straight, narrow, radial tubes, upon the upper regions of which the gonads are situated. The proboscis is wide and flask-shaped, and the mouth is provided with four prominent, crenulated lips. The color of the entoderm of the proboscis and tentacle bulbs is ochre-yellow, or reddish-brown. Several specimens were found at the Tortugas, Florida, late in June and early in July, 1898, and in June, 1899.

It is evident that this species has been noticed by Fewkes, 1882, under the name of "Tiaropsis diademata." The species is quite distinct from T. diademata, however, for it is smaller, possesses fewer tentacles, and is of a different color; moreover the bell of the young medusa is very much flatter than is that of T. diademata in a corresponding stage of development. The Tortugas form is closely allied to T. roseæ of the Fiji Islands ; and it also bears some resemblance to T. mediterranea, Metschnikoff (1886; Arbeit Zool. Inst. Wien. Bd. VI. p. 239, Taf. I. Figs. 6–8).

OCEANIA, Peron and Lesueur, 1809.

Oceania McCradyi.

Figs. 56–59, Plate 21.

Epenthesis McCradyi, Brooks, W. K., 1888, Studies Johns Hopkins Univ. Biol. Lab., Vol. IV. pp. 147–162, Pls. 13–15.

We present some colored figures of this remarkable medusa which develops hydroid-blastostyles upon its gonads. It has been found by Brooks among the Bahama Islands, and by Bigelow off the Florida Coast. We found it at the Tortugas, Florida, in July, 1898. Brooks, 1888, claims to have found the hydroid of this species.

Oceania magnifica, nov. sp.

Figs. 18, 18a, Plate 9.

Specific Characters. — The bell is thin and flat and 14 mm. in diameter. There are 32 slender tentacles of short length. There are 64 otocysts, 2 between each successive pair of tentacles. Each otocyst contains a single, spherical otolith. The velum is small. There are 4 straight, narrow, radial tubes. The gonads are developed upon the distal portion of these tubes near to the circular canal. The proboscis is short, and there are 4 sharply curled lips. The color of the entoderm of the proboscis and tentacle bulbs is intense green, while the ectoderm of the proboscis and of the genital organs is usually rich purple.

Several specimens were found at the Tortugas, Florida, in June, 1897, and a large number during the summers of 1898 and 1899.

Oceania globosa, nov. sp.

Figs. 19, 19^a, Plate 9.

Specific Characters. — The bell is globular in form, 14 mm. in diameter, The cavity of the bell is shallow so that the gelatinous substance is very thick. There are 32 large tentacles and 32 rudimentary ones. There are 64 otocysts alternating with the tentacles. Each otocyst contains 3–5 spherical otoliths (Figure 19^a). There are 4 straight, narrow, radial canals. The 4 gonads are situated upon the distal portions of the canals. The proboscis is very short and there are 4 prominent lips. The color of the entoderm of the proboscis and tentacle bulbs is light drab.

Single specimen found at Tortugas, June 16, 1897.

Oceania gelatinosa, nov. sp.

Figs. 20, 20^a, Plate 10.

Specific Characters. — The bell is 7 mm. high and 3.3 mm. in diameter. The gelatinous substance of the upper portion of the bell is very thick. There are 16 well-developed tentacles and 16 rudimentary ones that may develop later. There are 32 otocysts alternating with the tentacles. Each of these otocysts contains 3–5 spherical otoliths (Figure 20^a). The velum is prominent. There are 4 radial canals, in the upper or proximal portion of which the gonads are developed. The proboscis is long and slender and there are 4 prominent lips. The color of the entoderm of the proboscis and tentacle bulbs is light drab, or opaque white.

A specimen was found at the Tortugas, Florida, on June 14, 1897, and several others during the summer of 1899.

Oceania discoida, nov. sp.

Figs. 53-55, Plate 20.

Specific Characters. — The bell is quite flat, with conically sloping sides, and is 4 mm. in diameter. There are 16 short marginal tentacles with large basal bulbs. There are usually 3 otocysts between each successive pair of tentacles (see Figure 55). The velum is well developed. There are 4 straight radial tubes, upon the greater portion of the length of which the gonads are situated. In the case of the female the eggs are very large and prominent. The proboscis is urn-shaped and there are 4 recurved lips. The proboscis, gonads, and tentacle bulbs are yellow, or yellow-green. The entodermal supporting lamella of the bell is often of a delicate shade of green. The medusa is easily distinguished from the other species of Oceania at the Tortugas by the circumstance that it is very small in size, the bell is conical in shape, and the gonads are large and prominent. It is quite common throughout the summer.

Obelia, sp.

Eucope, sp. Agassiz, A., 1881, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. IX. p. 149.

A very few specimens of the medusa of an Obelia were found at the Tortugas, Florida, late in June, 1898. The bell was disk-shaped and about 3 mm. in diameter. There were 96 tentacles and 8 otocysts. The gonads were large and spherical, and much distended with ova. The bell was colorless. Not having seen the hydroid stock we are unable to determine whether or not this Obelia is identical with any of the forms found at Newport, R. I.

EPENTHESIS, McCRADY, 1857.

Epenthesis folleata, McCRADY.

Fig. 139, Plate 41.

Epenthesis folleata, McCrady, J., 1857, Gymn. Charleston Harbor, p. 89.
Oceania folleata, Agassiz, A., 1865, North Amer. Acal., p. 70.

Specific Characters. — Adult medusa. The bell is usually flatter than a hemisphere, and is about 5 mm. in diameter. Its cavity is shallow, and the bell walls diminish in thickness very gradually from the summit towards the margin. There are 16 slender tentacles with well-developed basal bulbs. 16 otocysts alternate in position with the tentacles. Each otocyst contains a single spherical otolith. The velum is well developed. There are 4 slender, straight, radial canals and a narrow ring-canal. The proboscis is short and simple and there are 4 slightly recurved lips. The 4 gonads are short and linear and are developed upon the 4 radial canals near the circular canal. In the young medusa they are found higher up upon the radial canals, but they migrate centrifugally as development proceeds. The entoderm of the proboscis, tentacle bulbs, and gonads is of a decided green color. This medusa is very common at the Tortugas, Florida, during the spring months, but becomes rare after the first of June. We have found it abundant in the Bahamas during the winter months. It is rare at Charleston, South Carolina, but Brooks found both hydroid and medusa at Beaufort, North Carolina.

EUCOPIUM, HAECKEL, 1879.

Eucopium parvigastrum, nov. sp.

Fig. 140, Plate 42.

Specific Characters. — The bell is half egg-shaped and is 1 mm. in height. There is a very small apical projection. There are 4 very small radially situated tentacles, which are hardly more than mere tentacle bulbs. There are 8 otocysts, 2 in each quadrant. Each otocyst contains a single spherical otolith. The velum is well developed. There are 4 straight, narrow, radial canals, and a slender circular vessel. The proboscis is very small, and is a mere tube, cruciform in cross-section and provided with 4 simple lips. The gonads occupy 4 linear swollen regions near the mid-regions of the 4 radial canals. The entoderm of the tentacle bulbs, gonads, and proboscis is of a decided brown color. This medusa was quite common at the Tortugas, Florida, late in June, 1899.

The very small proboscis and marginal tentacles as well as the remarkable swollen condition of the gonads in this medusa foreshadow the condition of Agastra mira (Hartlaub, 1897; Wissen. Meeresuntersuch. Biol. Anstalt Helgoland, Neue Folge, Bd. II. p. 504, Taf. XII. Fig. 10), where there is no trace either of proboscis or tentacles.

PSEUDOCLYTIA, nov. gen.

Pseudoclytia pentata, nov. sp.

Figs. 24-26, Plate 12; Figs. 35, 35a, Plate 15; Figs. 131, 132, Plate 39.

Generic Characters. — Pseudoclytia. Eucopidæ with numerous simple tentacles (20 in this species). Otocysts alternating with the equally numerous tentacles. 5 simple radial canals, 72° apart. 5 gonads situated upon the 5 radial canals. The proboscis lacks a peduncle and is provided with 5 simple lips.

Specific Characters. — Adult medusa. The bell is flatter than a hemisphere and is 8–13 mm. in diameter. There are 20 simple tentacles with well-developed basal bulbs. Each of these tentacles is a little less than half as long as the bell height. There are no lateral or marginal cirri. There are 20 otocysts which alternate in position with the 20 tentacles. Each otocyst contains a single spherical otolith (Figure 26). The velum is well developed. There are 5 straight, narrow, radial canals 72° apart. The 5 gonads are situated upon the radial canals at points midway between the proboscis and the bell margin (Figures 35, 131). In the female the ova are large and prominent, and when immature are seen to have a well-defined nucleus and nucleolus (Figures 35a, 131). The proboscis is flask-shaped and there are 5 simple recurved lips. The entoderm of the proboscis, gonads, and tentacle bulbs is usually slightly milky in color, with a few scattered cinnamon-colored granules. Occasionally an individual is met with in which these cinnamon-colored granules are developed to such an extent that the medusa displays a brick-red color (Figure 35). In most individuals, however, the colored granules are so faint as to be almost imperceptible. In some individuals there is a more or less decided green spot in the entoderm of each tentacle bulb (Figures 131, 132).

This medusa is very common throughout the summer months at the Tortugas, Florida. On July 22, 1898, a great swarm of them appeared, and were so abundant that one could not dip up a bucketful of sea-water without capturing several specimens; and two such swarms came in the summer of 1899.

This is the only Hydromedusa known which is normally formed upon the plan of five (pentamerous). It seems very probable that it has arisen, phylogenetically, as a sport from some species of Epenthesis or Oceania, some individuals of which made their appearance with 5 radial canals instead of 4; and these abnormal individuals succeeded in perpetuating a new species. Bateson (1894; Materials for the Study of Variation, p. 425) calls attention to an abnormal specimen of Sarsia mirabilis having five complete segments, and says that "there is perhaps in the whole range of natural history no more striking case of the Discontinuity and perfection of Meristic Variation. In the case of Eucope (Obelia) it has been shown by Agassiz and Woodworth (1896; Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXX. p. 121–150, 9 Plates) that among 3,917 medusæ 9 had three radial canals, 20 had five, and 3 had six radial canals. It thus appears that in Obelia the tendency to produce sports having 5 radial canals is about twice as great as that to produce individuals with any other number of canals. Yet sports of Obelia with 5 radial canals have not succeeded in perpetuating a new species.

I have made careful observations of 1000 individuals of Pseudoclytia pentata, and find that 70.3% are normal (*i. e.* have 5 canals 72° apart, 5 gonads, and 5 lips to the proboscis). The remaining 29.7% are abnormal in some respects, and a large number of the abnormalities tend toward the ancestral condition of 4 canals and 4 lips. The medusa is very much more variable than the 4-rayed Epenthesis folleata at the Tortugas, and its greater variability *may* be due to the fact that being a new form it displays a greater tendency toward variability in various directions. This question will, however, be made the subject of a special paper.

MULTIORALIS, nov. gen.

Multioralis ovalis, nov. sp.

Figs. 129, 130, Plate 39.

Generic Characters. — Multioralis. Leptomedusæ having a circular canal, and a single, simple chymiferous canal which extends across the sub-umbrella. A number of separate manubria are situated upon the chymiferous canal.

Specific Characters. — Adult medusa. The bell is quite flat, and is elliptical in outline, the major axis being 4 mm. and the minor 2.4 mm. The gelatinous substance is not very thick and is quite flexible. There are 20–25 short, simple, coiled tentacles with well-developed basal bulbs. These tentacles are only about one half as long as the minor axis of the bell. There are no lateral or marginal cirri. The otocysts are slightly more numerous than the tentacles; usually one, but occasionally two, being found between each successive pair of tentacles. Each otocyst contains a single spherical otolith. The velum is simple and quite broad. There is a slender circular vessel, and a single straight chymiferous canal extends along the major axis of the bell. In the oldest medusæ observed there were 4 manubria. Two equally developed large manubria were situated on either side of the centre of the sub-umbrella, upon the chymiferous canal; while two small manubria were found upon the same canal centrifugally away from the larger manubria. There was thus no manubrium at the centre of the sub-umbrella. There were two small gonads upon the chymiferous canal immediately centrifugal from the small manubria. The entoderm of the manubria and of the basal bulbs of the tentacles is of an opaque glistening white. The supporting lamella of the bell is of a delicate green.

Young Medusa. — In the youngest medusa observed, there were but 2 manubria situated upon the chymiferous canal on either side of the centre of the disk. The major axis of the bell was 2.5 mm. and there was no trace of gonads. About a dozen specimens of this medusa were captured at the Tortugas, Florida, from June 30–July 2, 1899.

It seems possible that the bell of the large medusæ may divide by transverse fission, for one individual was found in which there was a decided notch in the bell-margin extending inward in the plane passing through the centre of the sub-umbrella perpendicular to the main chymiferous tube. This notch appeared, however, upon only one side of the bell and may have been due to an accident. The main chymiferous canal is of course equivalent, morphologically, to two diametrically opposed radial canals.

EUCHEILOTA, McCrady, 1857.

Eucheilota ventricularis, McCrady.

Fig. 128, Plate 38.

Eucheilota ventricularis, McCrady, J., 1857, Gymn. Charleston Harbor, p. 85, Pl. 11, Figs. 1, 2; Pl. 12, Figs. 1–3.

This medusa is quite rare at the Tortugas, Florida, and not more than a dozen specimens were obtained. They were remarkable in that the entoderm of the tentacle bulbs and proboscis was of a decided green color. Each otocyst contained 2–4 spherical otoliths. In specimens 2 mm. in diameter there were as yet no gonads upon the radial canals.

Eucheilota bermudensis.

Oceanopsis bermudensis, Fewkes, J. W., 1883, Bull. Mus. Comp. Zoöl., Vol. XI. p. 86, Pl. I. Figs. 8–10.

Specific Characters. — Adult medusa. The bell is not quite hemispherical, the sides being relatively straight and sloping and the top quite flat. It is about 6 mm. in diameter. There are 8 tentacles, 4 radial and 4 interradial. These tentacles are only about one third as long as the bell diameter, and are thickly covered with nematocysts. Their basal bulbs are large, and are each flanked by a pair of short, coiled, nematocyst-bearing cirri. In addition to these there are normally about 8 other cirri in each quadrant, and scattered between them are 8 otocysts. Thus the medusa has 32 otocysts and 48 cirri. Each otocyst is of small size and contains a single spherical otolith. The velum is well developed. There are 4 straight, narrow, radial canals, and a simple circular vessel. The proboscis is short, but wide, and there are 4 cruciform, slightly recurved lips. There is no peduncle. The 4 gonads are found upon the 4 radial canals near the proboscis. These are visible in young medusæ about 1.5 mm. in diameter; and in the adult they become quite large and swollen, the ova being distinctly seen lying along the side of the canal. The entoderm of the proboscis gonads and tentacle bulbs is grass green, and the supporting lamella of the bell is tinged with the same color. This medusa was quite common at the Tortugas, Florida, from June 17–25, 1899.

Young Medusa. — The youngest medusa was about 2 mm. in height and 1.5 mm. in diameter. It was very much in the condition described by Fewkes, 1883. There were 4 simple radially situated tentacles and 4 interradial tentacle bulbs. The interradial tentacle bulbs were flanked by lateral cirri, while the radial tentacle bulbs lacked these appendages. There were 4 otocysts, one upon the side of each of the interradial tentacle bulbs. Each otocyst contained a single spherical otolith. The gonads were already quite large, and lay along the 4 radial canals near the sides of the proboscis. The proboscis was short, and there were 4 simple lips.

Eucheilota paradoxica, nov. sp.

Figs. 134-136, Plate 40.

Specific Characters. — Adult medusa: the bell is somewhat fuller than a hemisphere and is 4 mm. in diameter. The gelatinous substance is of moderate thickness, and there is a very slight, blunt, aboral projection. There are 4 equally developed, radially situated tentacles. These tentacles are about as long as the bell height, but are usually carried coiled in a close helix. Their basal bulbs are elongate, and are hollow. The shafts of these tentacles are thickly covered with nematocysts. A pair of tightly coiled lateral cirri arise from the sides of each tentacle bulb. In addition to these well-developed tentacles there are 4 interradial, rudimentary tentacle bulbs which are flanked by lateral cirri. There are 8 otocysts, 2 in each quadrant. Each otocyst contains a single spherical otolith. The velum is well developed. There is a narrow circular vessel, and 4 straight simple radial canals. The proboscis is flask-shaped, and there is no peduncle. There are 4 simple cruciform lips. Medusa buds in various stages of development are found upon the 4 gonads, which are situated at the middle points of the 4 radial canals. These medusa buds first develop 2 diametrically opposed tentacles (Figure 135), but when about to be set free they have 4 equally developed tentacles as in the adult. They have, however, no trace of gonads, and the interradial tentacle bulbs are not provided with lateral cirri. Usually from 2–5 medusa buds in several stages are found upon each gonad. The entoderm of the proboscis gonads and tentacle bulbs is of a milky-green color.

This medusa was common at the Tortugas, Florida, in June, 1899.

This is the first and only Leptomedusa which has been observed to give rise to free medusa buds.

EUTIMA, McCrady, 1857.

Eutima mira, McCrady.

Eutima mira, McCrady, J., 1857, Gymn. Charleston Harbor, p. 88, Pl. XI. Figs. 8, 9.

This medusa is common throughout the summer at the Tortugas, Florida. It is also abundant at Charleston, South Carolina, and at Beaufort, North Carolina. Damaged specimens are occasionally drifted into Newport Harbor, Rhode Island, by the southerly winds, late in the summer.

EUTIMALPHES, Haeckel, 1879.

Eutimalphes cœrulea.

Figs. 22, 22ᵃ, Plate 11.

Eirene cœrulea, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV., p. 362.
Irene cœrulea, Haeckel, E., 1879, Syst. der Medusen, p. 203.

Specific Characters. — The bell is 10 mm. in diameter and a little broader than it is high. The gelatinous substance at the apex of the bell is quite thick, but becomes progressively thinner as one approaches the margin. There are about 32 short, slender, marginal tentacles, each one of which is furnished with small lateral cirri. In addition to the well-developed tentacles there are about 96 rudimentary tentacular swellings upon the bell margin. There are usually about three of these swellings between each successive pair of tentacles. (Figure 22^a.) There are 8 otocysts, 2 in each quadrant, and each one of them contains 3–5 spherical otoliths. There are 4 radial tubes. The velum is well developed. There are 4 linear, slightly convoluted gonads. They begin about halfway between the circular vessel and the peduncle, and extend to a point close to the proboscis. The peduncle is well developed and reaches slightly beyond the velar opening. The gastric portion of the proboscis is short and is furnished with 4 slightly fimbricated lips. The proboscis, gonads, and tentacle bulbs are opaque white. Common at the Bahamas and Tortugas in the spring and winter months.

EUTIMIUM, HAECKEL, 1879.

Eutimium serpentinum, nov. sp.

Figs. 69-72, Plate 23.

Specific Characters. — The bell is 10 mm. in diameter, and about 2½ times as broad as it is high. There are 4 radially situated tentacles; each being about as long as the bell diameter. There are no lateral or marginal cirri. The 8 otocysts are situated near to and on both sides of the radial tentacles. (Figure 70.) Each otocyst contains 4–8 spherical otoliths. The velum is well developed. There are 4 straight narrow radial tubes and a narrow circular vessel. The proboscis possesses a very long peduncle, which is about 3 times as long as the bell diameter. The upper region of the peduncle is conical in shape; then follows a long slender cylindrical region leading to the gastric part of the proboscis, which is urn-shaped with 4 slightly recurved lips. (Figure 71.) The 4 gonads are situated upon the long cylindrical portion of the peduncle, where they lie upon the radial canals. (Figure 72.) The proboscis, gonads, and tentacles are opaque bluish-white. Half a dozen specimens of this medusa were found at the Tortugas, Florida, late in July, 1898. It is closely allied to Eutimium elephas, Haeckel (1879; Syst. der Medusen, p. 190, Taf. XII. Figures 10–12), of the German Ocean.

PHORTIS, McCRADY, 1857.

Phortis lactea, nov. sp.

Fig. 133, Plate 40.

Specific Characters. — The bell is 5 mm. in diameter and the sides flange slightly outward at the margin. The gelatinous substance is of moderate thickness at the aboral pole, but becomes thin at the margin of the bell. There are about 18–22 short simple tentacles, the basal bulbs of which are large and swollen. These tentacles are only about one fifth as long as the bell diameter. There are no lateral or marginal cirri. The otocysts are slightly more numerous than the tentacles, there being at least one, and occasionally two, of these structures between each successive pair of tentacles. Each otocyst contains a single spherical otolith. The velum is well developed. There are 4 straight slender radial canals, which extend down the peduncle to the gastric portion of the proboscis. The peduncle is wide at its base, but not so wide as in Phortis pyramidalis. It extends for a short distance beyond the velar opening of the bell. The gastric portion of the proboscis is cruciform in cross-section and there are 4 simple recurved lips. The 4 gonads are situated upon the 4 radial canals a short distance above their junction with the circular vessel. Each gonad is linear, and in the female the ova are quite conspicuous. The gonads and the gastric portion of the proboscis are milky in color, while the tentacle bulbs are cream-colored with greenish entodermal granules. Found at the Tortugas, Florida, in June.

Phortis pyramidalis.

Figs. 21, 21ᵃ, Plate 10.

Eutima pyramidalis, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV., p. 363.

Specific Characters. — Adult medusa. The bell is slightly flatter than a hemisphere, and attains a diameter of about 35 mm. There are about 100 small slender tentacles, which lack lateral cirri. About 100 otocysts alternate with the equally numerous tentacles. Each otocyst contains a single spherical otolith. (Figure 21ᵃ.) There are 4 narrow radial canals. The proboscis is provided with a wide cone-shaped proboscis which fills most of the cavity of the bell, and projects outward for a considerable distance beyond the velar opening. The gastric portion of the proboscis is very small, and is provided with 4 delicately crenulated lips. The gonads are linear and are developed upon the centrifugal portions of the 4 radial canals near to the circular canal. The proboscis, tentacle bulbs, and gonads are of a delicate blue-green color. This medusa is very abundant among the Bahama and Tortugas Islands. At night, when disturbed, it glows with an intense blue-green phosphorescence which is far more brilliant than that of any other medusa that we have observed.

Young Medusa. — Phortis pyramidalis. In the youngest medusa observed the bell was higher than a hemisphere and 3 mm. in diameter. There was no peduncle to the proboscis, and the gelatinous substance of the bell was not very thick. There were 4 slender radial tubes and 16 tentacles, only 8 of which had attained to any length, the others being mere basal bulbs. There were about 8 otocysts, each containing a single spherical otolith. When the medusa is about 7 mm. in diameter, the bell is flatter than a hemisphere. The peduncle is well developed and extends beyond the velar opening. The gastric portion of the proboscis has grown very little and is relatively to size of the medusa much smaller than in the younger animal. There are 4 recurved lips. There are now about 32 tentacles and 16 otocysts.

ZYGODACTYLA, Brandt, 1835.

Zygodactyla cubana, nov. sp.

Figs. 84, 85, Plate 25.

Specific Characters. — Young medusa. The bell was quite flat and disk-shaped and 4.5 mm. in diameter. There were 8 long tentacles, 8 rudimentary, undeveloped tentacles, and 16 very small undeveloped tentacle bulbs, that probably develop later into tentacles. The tentacle bulbs possessed excretion papillæ and were further distinguished by the fact that there were two entodermal green pigment spots one on either side of the bulb (see Figure 85). These spots had the appearance of ocelli, but we do not venture to state that they are such. There were 32 otocysts, each containing one or two spherical otoliths. The velum was well developed. There were 16 radial canals, only 8 of which reached the circular vessel. The 8 others projected about halfway from the proboscis to the circular canal. The proboscis was wide and flask-shaped, and projected for a considerable distance beyond the velar opening. The 16 lips were recurved. The gonads were beginning to appear upon the radial canals. The entoderm of the proboscis and radial canals is sage-green. The entoderm of the tentacle bulbs was flesh-colored and the "ocelli" were green. Tortugas, Florida, July 25–29, 1898, and June, 1899.

Zygodactyla cyanea, Agassiz, L.

Figs. 23, 23a, Pl. 11; Figs. 33, 34, Pl. 15.

Zygodactyla cyanea, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 361.
Mesonema cyaneum, Haeckel, E., 1879, Syst. der Medusen, p. 227.

Specific Characters. — Adult medusa. None of our figures were drawn from full-grown medusæ. The bell is flatter than a hemisphere and is about 45 mm. in diameter (22 mm. in Figure 33). The gelatinous substance of the central part of the bell is very thick and there is a well-developed peduncle which projects downward into the cavity of the stomach. The peripheral zone of the bell is quite thin and flexible. There are 90–100 well-developed tentacles with large conical basal bulbs. Each tentacle bulb is hollow and is provided with a conical excretion papilla which projects outward (centrifugally). See Figure 34, Plate **15**. There are one or two (usually one) otocysts between each successive pair of tentacles. Each otocyst contains one or two spherical otoliths. The velum is well developed. There are 90–100 simple, straight radial tubes. The radial tubes do not extend down the peduncle of the proboscis, but empty into the stomach cavity at their highest point. The proboscis is wide and shallow, and does not protrude beyond the velar opening. The mouth is surrounded by numerous crenulated lips which are equal in number to the radial canals. The stomach is about two thirds as wide as the bell diameter. The gonads are linear, and occupy almost the whole length of the radial canals. The entoderm of the gonads, tentacle bulbs, and proboscis is blue-green. The medusa is very common off the Florida Coast both in summer and winter.

ÆQUOREA, Péron and Lesueur, 1809.

Æquorea floridana.

Rhegmatodes floridanus, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 361.

Specific Characters. — The bell is hemispherical and 25 mm. in diameter. The gelatinous substance of the bell is thick and of a tough consistency. There are 16 radial tubes and 64 well-developed marginal tentacles. The tentacle bulbs are large and hollow, and are provided each with one or two excretion papillæ, which project outward from the side of the bell. There are about 192 otocysts, three between each successive pair of tentacles. Each otocyst contains 2 spherical otoliths. The velum is well developed. The 16 gonads are developed upon the distal halves of the 16 radial canals. The surface of the mature gonads is slightly convoluted. The proboscis is wide and very shallow, and there are 16 slightly fimbricated lips. The gonads and the edge of the bell are milky-white. Common at the Tortugas and Bahamas in the spring months.

RHACOSTOMA, Agassiz, L., 1862.

Rhacostoma dispar, nov. sp.

Figs. 27-29, Pl. 13.

Specific Characters. — The bell is lens-shaped, and about 40 mm. broad and 20 mm. high. The cavity of the bell is remarkably small and shallow, so that the gelatinous substance is very thick. The velar opening of the bell is only about 5 mm. in diameter. There are about 8 very small rudimentary tentacles. There are 30–40 otocysts scattered between the tentacles. Each otocyst contains 3–5 oval-shaped otoliths (see Figure 29). There are no excretion papillæ. The velum is well developed. There are about 80 radial tubes, fully half of which end blindly without reaching the circular tube. The gonads are situated upon all of the radial tubes. They are linear, and their surfaces are slightly convoluted. They do not extend quite to the peripheri of the stomach, nor do they reach the circular canal. The proboscis is very wide, and may at times be protruded beyond the velar opening. There are about 80 small crenulated lips, which are apparently as numerous as the radial canals. The bell has a faint steel-blue tinge, and the genital organs are pink. A single specimen was found at the Tortugas, Florida, in June, 1897. This remarkable species is extremely inactive. Owing to the small size of the velum, it is of but little service in swimming, and the medusa makes use of the contractions of its widely open mouth in order to propel itself through the water.

GONIONEMUS, Agassiz, A., 1865.

Gonionemus aphrodite.

Cubaia aphrodite, Mayer, A. G., 1894, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXV. p. 237, Pl. II. Figs. 1–3.

This medusa is occasionally met with at the Tortugas, Florida, and an examination of mature individuals has convinced me that it belongs to the genus Gonionemus. The gonads consist of a series of finger-shaped, or papilliform, processes that are crowded alternately to one side and the other of the radial canal very much as in the species of Gonionemus found at Woods Holl, Massachusetts.

GONIONEMOIDES, nov. gen.

Gonionemoides geophila, nov. sp.

Figs. 6-11, Plates 3-5.

Generic Characters. — This genus is closely related to Gonionemus, but differs from it in that the marginal tentacles are of two distinct kinds, and arise at slightly different levels from the bell margin. One of these sets of tentacles is provided with nettling cells, and the other is furnished with adhesive suckers, as in Gonionemus. There are 4 radial canals, and the circular vessel is simple without centripetal canals. The gonads are papilliform and are situated upon the radial canals. There are numerous otocysts upon the bell margin.

Specific Characters. — Adult medusa, Figures 6–9. The bell is quite flat and disk-shaped, and is about 9.5 mm. in diameter. There are 64 marginal tentacles. 16 of these bear, each one, a suctorial disk upon the aboral sides near their distal extremities. The extreme distal ends of the tentacles are cone-shaped, and are bent sharply at a right angle to the main shaft of the tentacle, very much as is the case in Gonionemus vertens, A. Agassiz. These sucker-bearing tentacles arise at a level, a little above the bell margin. The remaining 48 tentacles all arise from the bell margin, at a lower level than do the sucker-bearing ones. They possess no suctorial disks, but instead are armed with rings of nematocyst capsules (Figure 6). These nematocyst-bearing tentacles are far more flexible than are the sucker-bearing ones.

There are 12 otocysts upon the bell margin, each one of which contains a single otolith situated within an elongate, oval cavity (see Figure 7). The velum is well developed. There are 4 straight radial tubes. The gonads occupy the distal halves of the radial tubes, but do not quite extend to the circular vessel. They present the appearance of a series of papilliform, or finger-shaped, processes that are crowded alternately to one side and the other of the radial tube, very much as is the case in Gonionemus vertens. The proboscis is a simple tube with 4 prominent lips. There are 4 radially situated green-colored spots upon the proboscis close to its junction with the 4 radial canals.

Young Medusa. — Figures 10, 11, Plate **5**. The youngest medusa observed was 1.7 mm. in diameter. The bell was high and quite thick, and its aboral surface was covered with nematocyst capsules. The 16 sucker-bearing tentacles were already present, although the suctorial disk was visible upon only 8 of them. Figure 11 is a side view of the end of one of these young tentacles showing the beginning of the formation of the suctorial disk. There were 7 otocysts present. The velum was very prominent. There were no traces of genital organs present. The proboscis possessed a distinct peduncle. The color of the genital organs, bell margin, and proboscis of this medusa is pearly white. The entoderm of the tentacle bulbs and of the radial tubes in the region of the gonads is green. The ocelli ? of the proboscis are green.

The adult medusa would frequently lie flat upon the bottom of the aquarium with its oral surface upward (Figure 9, Plate **4**). In this position the sucker-bearing tentacles would be stretched far out and the suckers would anchor the medusa to the bottom. The nematocystic tentacles, on the other hand, would wave freely upward apparently in position for the capture of prey. When disturbed the medusa would swim actively about for a few moments, and then reassume its characteristic position of rest.

This medusa was common at Key West from May 27–June 10, 1897.

HALICALYX, FEWKES, 1882.

Halicalyx tenuis, FEWKES.

Figs. 12, 13, Plates 5, 6.

Halicalyx tenuis, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. IX. p. 277, Pl. VII. Fig. 15.

Generic Characters. — This genus is closely allied to Gonionemoides, but differs from it in that none of the tentacles bear suctorial disks. The tentacles are of two distinct kinds and arise at different levels from the bell margin. The circular vessel gives off blind centripetal branches. There are otocysts at the bases of the tentacles. Tentacles numerous.

Specific Characters. — The bell is 25 mm. in diameter and is hemispherical. It is quite thick at the aboral pole, but becomes constantly thinner as one approaches the margin. The gelatinous substance is of very rigid consistency.

There are about 50 tentacles, and 64 short, blunt papillæ upon the bell margin. 32 of the tentacles arise from the side of the bell at a little distance above the margin. They are short and stiff and stand out sharply at right angles to the bell (see Figure 3). These tentacles are sprinkled over with wart-like protuberances of a deep purple color. A pair of otocysts, each containing a single otolith, are situated at the base of each of these stiff tentacles. Thus the medusa possesses 64 otocysts. In addition to the stiff tentacles there are about 20 others that are long and flexible, and arise from the bell margin. They are covered with rings of nematocyst cells closely coiled in a helical manner (see Figure 12). These tentacles are very flexible and are constantly being expanded to a length of 4–5 times the diameter of the bell and then contracted with a sudden jerk. The velum is small. There are 4 straight, narrow, radial tubes. The circular vessel is peculiar in that it gives off blindly ending, centripetal branches or diverticulæ, that penetrate inward into the substance of the bell. There are in all 28 side branches. 4 of these are each about half as long as the radial tube. 8 others are only one quarter as long as this, and the 16 remaining ones are still shorter. These diverticulæ are situated immediately above the short, stiff tentacles (see Figure 13). The gonads are found occupying the distal half of the radial canals, but do not reach quite to the bell margin. They hang downward into the bell cavity as a complex system of finger-shaped papillæ. The proboscis is very slender and the lips prominent. It extends for about three quarters of the distance of the height of the bell cavity. The gelatinous substance of the bell is slightly greenish in color. The entoderm of the proboscis, genital organs, circular tube, and tentacles is opaque yellow-green and reddish purple. There are 4 reddish-purple spots upon the proboscis just between the radial canals.

This medusa was common at Key West from May 27–June 10, 1897. It was extremely active in all of its movements and wonderfully hardy in captivity. One specimen lived for more than a week in a small glass bowl, the water of which was not changed. It seems probable that both this species and Gonionemoides geophila prefer the muddy and impure waters of the Florida Coast, for while they were both common at Key West, they were not seen at the Tortugas either in 1897, 1898, or 1899.

LIRIOPE, Lesson, 1843.

Liriope scutigera, McCrady.

Liriope scutigera, McCrady, J., 1857, Gymn. Charleston Harbor, p. 106.
Xanthea scutigera, Haeckel, E., 1864, Geryoniden, p. 24.
Liriantha scutigera, Haeckel, E., 1879, Syst. der Medusen, p. 287.

This medusa is not very common at the Tortugas, Florida. It is quite abundant at Charleston, South Carolina, and we have taken it at various places among the Bahama Islands, and off the Cuban Coast, during the winter months.

GLOSSOCODON, Haeckel, 1864.

Glossocodon tenuirostris, Fewkes.

Figs. 75-78, Plate 24.

Liriope tenuirostris, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. p. 365.
Glossocodon tenuirostris, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. IX. p. 278, Pl. VII. Figs. 1–9.
Liriope cerasiformis? Maas, O., 1893, Ergeb. der Plankton Exped., Bd. II. K. Ç., p. 35, Taf. II. Fig, 5. 6.

This medusa is common at the Tortugas, Florida; as indeed it is also among the Bahama Islands and along the Cuban Coast. It is met with in considerable numbers in Charleston Harbor, South Carolina; and occasionally a damaged individual is drifted into Newport Harbor, Rhode Island, by the southerly winds late in the summer months.

AGLAURA, Péron and Lesueur, 1809.

Aglaura hemistoma, Péron and Lesueur.

Figs. 79, 80, Plate 25.

Aglaura hemistoma, Péron, F., et Lesueur, C. A., 1809, Tableau des Méduses, p. 351, No. 73.
Aglaura Péronii, Leuckart, R., 1856, Archiv für Naturges. Jahrg. 22, p. 10, Taf. I. Figs 5–7.

This medusa is occasionally met with in June at the Tortugas, Florida. It is found also in the Mediterranean and is widely distributed throughout the tropical regions of the Atlantic (see Maas, O., 1893, Die Craspedoten Medusen der Plankton Expedition, Taf. VII.). A very closely allied species is found in the Tropical Pacific (see Agassiz and Mayer, 1898; Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 166). One figure is drawn from a specimen obtained at the Tortugas, Florida.

Aglaura hemistoma, var. Nausicaa, Haeckel.

Aglaura Nausicaa, Haeckel, E., 1879, Syst. der Medusen, p. 274, Taf. XVI. Fig. 1.
Aglaura vitrea, Fewkes, J. W., 1882, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. IX. p. 277, Pl. VII. Fig. 10.
Aglaura hemistoma, var. Nausicaa, Maas, O., 1892, Die Craspedoten Medusen der Plankton Expedition, Bd. II. K. C., p. 26.

This variety is occasionally met with at the Tortugas, Florida.

CUNOCTANTHA, Haeckel, 1879.

Cunoctantha incisa, nov. sp.

Figs. 145, 146, Plate 44.

Specific Characters. — The bell is slightly flatter than a hemisphere and is about 5 mm. in diameter. There is a slight apical projection, which is solid. 8 stiff tentacles arise from the sides of the bell, about halfway between the margin and the apex. These tentacles are provided with well-developed conical insertions, and their entodermal cells are disk-shaped and highly vacuolated. There is a well-developed peronium beneath each tentacle. The tentacles are all of equal length, and are about three quarters as long as the bell diameter. The ex-umbrella extends outwards in 8 lobes, which are held together in a web formed of the ascending velum. These are 24 pear-shaped marginal sense-organs, each containing a crystalline otolith and surrounded by a sensory pad bearing delicate bristles. The lower velum is well developed. The proboscis is flat and the stomach cavity is small. The mouth is a simple opening without prominent lips. The stomach gives rise to 8 pouches which extend outward in the radii of the 8 tentacles. The incisions between these pouches are deeper than in Cunoctantha octonaria of Charleston Harbor. The entoderm of the tentacles, and sometimes of the stomach, is green. Two specimens of this medusa were found at the Tortugas, Florida, late in May, 1899.

ÆGINELLA, Haeckel, 1879.

Æginella dissonema, Haeckel.

Figs. 30-32, Plate 14.

Æginella dissonema, Haeckel, E., 1879, Syst. der Medusen, p. 340, Taf. XX. Fig. 16
Æginella dissonema, Agassiz, A., and Mayer, A. G., 1899, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 166.

Specific Characters. — The bell is 3 mm. in diameter, and has the form of a frustum of a cone with rounded apex. It is a little wider than it is high. There are two long tentacles that arise from the sides of the bell at about ¾ of the distance from the margin to the apex. These tentacles are quite stiff and incapable of contraction. They are carried trailing behind the medusa in two straight parallel lines, and are about 3 times as long as the bell height. The entodermal core of each tentacle consists in a row of disk-shaped, highly vacuolated cells. (See Figure 31.) In addition to the long tentacles there are two very small protuberances (t. Figure 30) that arise from the bell margin, at the foot of the pair of peronial tubes that are situated 90° from the large tentacles. Haeckel, 1879, does not mention or figure these protuberances, and it seems probable that they may be absent in some individuals, for we did not observe them in specimens of Æginella dissonema from the Fiji Islands. In addition to the above-mentioned protuberances there are 4 small interradial swellings situated upon the bell margin. There are 8 sensory clubs, 2 in each quadrant (see Figure 32), each one of which contains a single spherical otolith. The velum is large and powerful and is constantly contracting and expanding with great rapidity. There are 4 peronial double canals, each canal being divided into two by means of a longitudinal septum. The proboscis is small and flat, and the mouth is a simple circular opening. There are 8 interradial pouches that extend outward from the stomach into the substance of the bell. The gonads are developed upon these pouches and in the specimen here figured they contained immature ova. The color of the entoderm of the proboscis and of portions of the entodermal core of the tentacles is intense golden-green. The gonads in the specimens described by Haeckel were rose-red; in ours they were colorless.

A single specimen was found at the Tortugas, Florida, June 19, 1897. This medusa appears to be very widely distributed. Haeckel found it at the Canary Islands, and we found it in Suva Harbor, Fiji Islands, in January, 1898.

II. SCYPHOMEDUSÆ.

NAUSITHOË, Kölliker, 1853.

Nausithoë punctata, Kölliker.

Figs. 67, 68, Plate 23; Figs. 87, 88, Plate 26.

Nausithoë punctata, Kölliker, A., 1853, Zeit für Wissen. Zoöl., Bd. IV. p. 323.
Nausithoë punctata (Marginata albida), Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. pp. 122, 167.
Nausithoë albida, Carus, V., 1857, Icones Zoötom., Taf. II., Figs. 17, 22, 23.

Specific Characters. — Adult medusa. The umbrella is quite flat and is about 9 mm. in diameter. There are 8 stiff tentacles, each one of which is about ¾ as long as the bell diameter. The main portion of the entodermal core of each tentacle is solid, but as Vanhöffen, 1892, has shown, the basal bulbs of the tentacles are hollow and connected with the adjacent lappet-pouches. There are 8 marginal sense-organs that alternate with the 8 tentacles. As the Hertwigs (1878, Sinnesorgan der Medusen, Figure 2, Plate 9) and Claus (1883, Organ. Entwick. Medusen, Figure 47, Plate 7) have shown, each sense-organ consists of an ectodermal eye, provided with a lens and with nerve fibres; and also of an entodermal otocyst containing a number of otoliths. (See Figure 68, Plate 23.) The 16 marginal lappets are long and flexible, and it is by means of their movements that the medusa is enabled to swim through the water with great rapidity. 16 diverticulæ or pouches from the stomach enter the 16 lappets. Each of these pouches is simple, and does not give rise to any system of canals ramifying through the lappets. The mouth is a simple cruciform opening and there are no oral appendages, or palps. The gastro-vascular cavity is a wide space occupying the whole centre of the umbrella and extending outward into the lappets to form the 16 lappet-pouches. There are 4 groups of gastric cirri, situated in such manner that the 2 diameters passing through them are 45° apart from the 2 diameters passing through the cross formed by the lips of the mouth. All 4 of these diameters pass through the marginal sense-organs. There are about 6 tentaculæ in each group of gastric cirri, thus making in all about 24 gastric tentaculæ. The 8 gonads are of entodermal formation, and are found in the 8 tentacular radii. As Claus, 1883, has shown, each one is formed from a pocket-like fold of the entoderm. A band of circular muscles is found in the ectoderm of the sub-umbrella, and radial muscle fibres run out from this band into the 16 marginal lappets. The color of this medusa is quite variable. The gelatinous substance of the bell is usually bluish white or brownish. The gonads are brownish red or, in the case of the males, bright yellow rosin-colored pigment spots are found in the ectoderm of the ex-umbrella, especially upon the lappets. These rosin-colored spots are due to small crystals (see Claus, 1883; Figure 44, Taf. VI.).

A young ephyra of this species (see Figures 67, 68; Plate **23**) was found by us near Flamingo Key, Bahama Islands, Feb. 9, 1893. It was 2 mm. in diameter. There were as yet no marginal tentacles. The otocysts each contained 5–6 oval otoliths. There were only 4 gastric cirri. A slightly older ephyra has been figured by Claus, 1883; Figure 48, Taf. VII.

This medusa is common in the Mediterranean, and is also found among the Bahama and Tortugas Islands. It was described by Vanhöffen, 1893, from near the mouth of the Amazon River. A *very* closely allied species was found by us in the Fiji Islands, Pacific Ocean.

LINERGES, Haeckel, 1880.

Linerges mercurius, Haeckel.

Linerges mercurius, Haeckel, E., 1880, Syst. der Medusen, p. 495, Taf. XXIX. Figs. 4–6.
Linerges pegasus ? Haeckel, E., 1880, Syst. der Medusen, p. 495.

Vast numbers of ephyræ of this medusa are found among the Bahama Islands and along the Florida Coast in March; and the mature medusæ are very abundant in June. At times these creatures appear in such numbers that hundreds are captured in every haul of the tow net. They congregate in great windrows, remain abundant for a few days, and then disappear for an indefinite period.

DACTYLOMETRA, Agassiz, L., 1862.

Dactylometra lactea, L. Agassiz.

Chrysaora lactea, Eschscholtz, F., 1829, Syst. der Acalephen, p. 81, Taf. VII. Fig. 3.
Dactylometra lactea, Agassiz, L., 1862, Cont. Nat. Hist. U. S., Vol. IV. pp. 125, 126, 166.
Dactylometra lactea, Agassiz, A., and Mayer, A. G., 1898, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 7, Pls. XII., XIII., and Fig. 10, Pl. VII.

This medusa is extremely common in Havana Harbor, Cuba, in February, where it swims upon the surface during the afternoon hours. It has been described by Eschscholtz from the Bay of Rio Janeiro, Brazil. It is occasionally found at the Tortugas, Florida.

AURELIA, Péron and Lesueur, 1809.

Aurelia habanensis, nov. sp.

Figs. 73, 74, Plate 24; Fig. 86, Plate 26.

Specific Characters. — Adult medusa. The bell is 240 mm. in diameter. It is disk-shaped, and the gelatinous substance is quite thick. There are 8 simple marginal lappets, which bear upon their dorsal surfaces, at a slight distance above the bell margin, a row of numerous short tentacles. There are 8 marginal sense-organs that are deeply set within niches situated between the marginal lappets. The radiating chymiferous tubes are very similar to those of Aurelia flavidula, Péron and Lesueur. The mouth-arms, or palps, are long and narrow and extend almost to the bell margin. Their free edges are not lined with a fringe of tentacles as in Aurelia flavidula, but instead are covered with wart-like clusters of nematocyst cells (see Figures 73, 74, Plate **24**). This, indeed, constitutes the principal difference between this species and Aurelia flavidula. The 4 gonads are horseshoe-shaped and there are 4 subgenital pits. Both the gonads and subgenital pits are smaller than in Aurelia flavidula. The gelatinous substance of the bell is bluish white in color. The genital organs of the males are pink, and of the females white in color. The basal bulbs of the marginal tentacles are often pink.

This medusa is extremely abundant in Havana Harbor, Cuba, in February. It makes its appearance at the Tortugas in August, but we do not know whether it is found also at Havana at that time or not.

While in Havana Harbor in February, 1893, we had the opportunity of observing the curious habits of this medusa. During the morning hours not one was to be seen, but at about four o'clock in the afternoon they began to appear in great numbers, and continued to be seen until long after nightfall.

This species is quite distinct from Aurelia marginalis, L. Agassiz (1862;

p. 86). In Aurelia marginalis the gonads are very large and occupy at least one half of the whole diameter of the disk, so that the distance from the peripheral outline of these organs to the margin of the disk is as great, if not greater, than that to the centre of the disk. The mouth-arms, on the contrary, are comparatively small. In Aurelia habanensis the gonads never occupy more than one third of the diameter of the disk, and the mouth-arms are long and slender.

CHARYBDEA, Péron and Lesueur, 1809.

Charybdea aurifera, nov. sp.

Figs. 81-83, Plate 25.

Specific Characters. — Young medusa. Only one specimen of this medusa was found at the Tortugas, Florida, August 6, 1898. The bell was 2 mm. in height and a little higher than it was broad. The external surface of the bell was covered irregularly with numerous wart-like clusters of nematocyst cells. The 4 interradial tentacles were evidently very immature, and consisted of small knob-like protuberances from the bell margin. They were hollow and were in communication with the general gastro-vascular cavities of the bell. The 4 sense-organs, or rhopalia, arose from 4 radially situated niches, found upon the sides of the bell at a little distance above the margin. It should be noted, however, that although the rhopalia appear to arise at some distance above the bell margin, they are morphologically homologous with appendages of the bell margin. Each rhopalium arises from a niche in the side of the bell, and consists in a stalk-shaped body, bearing upon its distal end a knob-shaped portion which, in turn, contains the otolith and eye-spots. There are 5 eyes in each rhopalium; one of these is large and median, and the other 4 are smaller and paired (see Figures 82, 83). They are so situated that they may look inward towards the bell cavity. These eyes are ectodermal structures, and possess a lens and a layer of pigment cells. The otolith, on the other hand, is entodermal in origin and consists in a mass of glistening white granules. The velarium is well developed, and is supported by means of 4 partitions, or frenulæ (*f*, Figure 81), that suspend it from the sub-umbrella. The proboscis is wide and flask-shaped, and there are 4 quadratic lips. 4 long gastric cirri, one in each interradius, extend downwards into the stomach cavity. A highly refractive band of muscle fibres ? (*m s*, Figure 81) extend down the middle line of each radius of the bell to the rhopalia. The gelatinous substance of the bell possesses a bluish tinge. The nematocyst cells of the exumbrella, and also the proboscis, rhopalia, and tentacles are of a decided amber color.

Although careful search was made for them, no velar canals were observed. It is probable that these may develop at a later stage.

Charybdea punctata.

Tamoya punctata, Fewkes, J. W., 1883, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XI. p. 84, Figs. 4–6, Pl. I.

A single young medusa of this species was found at the Tortugas, Florida, on May 24, 1899. It was very nearly in the same state of development as the medusæ described by Fewkes, 1883, from the Bermuda Islands. The adult medusa has not been found.

CASSIOPEA, Péron and Lesueur, 1809.

Cassiopea frondosa, Lamarck.

Medusa frondosa, Pallas, P. S., 1774, Spicilegia Zoölog., Fasc. X. pp. 29, 30, Pl. 2, Figs. 1–3.

Cassiopea frondosa, Lamarck, J. de, 1817, Hist. Nat. Anim. sans Vert., Tom. II. p. 512.

Cassiopea pallasii, Péron, F., et Lesueur, C. A., 1809, Tableau des Meduses, p. 357, Nr. 85.

Polyclonia frondosa, Agassiz, L., 1860, Cont. Nat. Hist. U. S., Vol. III. Pls. 13, 13^a.

This medusa is very abundant at the Tortugas and along the Florida Reefs early in the spring, but is not seen during the summer months.

III. SIPHONOPHORÆ.

VELELLA, Bosc, 1802.

Velella mutica, Bosc.

Medusa velella, Linné, 1767, Systema Naturæ, Ed. XII. p. 1098.

Velella mutica, Bosc, L. A. G., 1802, Hist. Nat. d. Vers., Tom. II. p. 158.

Velella mutica, Agassiz, A., 1883, Mem. Mus. Comp. Zoöl. at Harvard Coll., Vol. VIII. No. 2, p. 2, Pls. I.–VI. 91 Figures.

Armenista mutica, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl. Vol. XXVIII. p. 84.

This Siphonophore appears occasionally in great numbers at the Tortugas, Florida, especially when southerly breezes drive the surface waters of the Gulf Stream upon the Florida Reefs. It is common among the Bahama Islands and along the Cuban coast, and isolated individuals are often carried far to the northward by the Gulf Stream, specimens having been taken in Newport Harbor, Rhode Island.

PORPITA, Lamarck, 1816.

Porpita Linnæana, Lesson.

Porpita Linnæana, Lesson, R. P., 1843, Hist. Nat. des Zoöph. Acal., p. 588.

This Siphonophore is met with occasionally at the Tortugas, Florida. It often occurs in vast swarms, which appear at irregular intervals, all along the coast of the United States from the Tortugas to North Carolina. A single specimen was found by A. Agassiz, in Newport Harbor, Rhode Island, in 1875.

RHIZOPHYSA, Péron and Lesueur, 1809.

Rhizophysa Murrayana, Chun.

Rhizophysa filiformis? Gegenbaur, C., 1854, Zeit. für Wissen. Zoöl., Bd. V. p. 324, Taf. XVIII. Figs. 5–11.

Cannophysa Murrayana, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 324, Pl. XXIV. Figs. 1–9.

Cannophysa Eysenhardtii, Mayer, A. G., 1894, Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. XXV. p. 239, Pl. III. Figs. 1, 2, 4.

Rhizophysa Murrayana, Chun, C., 1897, Siphonophoren der Plankton Expedition, p. 84.

This Siphonophore has been found by us among the Bahama Islands and off the Cuban coast, and a single damaged specimen was obtained at the Tortugas, Florida. It has been obtained by Haeckel, 1888, at the Canaries, and by Chun, 1897, in the Tropical Atlantic. The Mediterranean species R. filiformis of Gegenbaur, 1854, is certainly very closely allied, if not identical with the Atlantic form.

Rhizophysa Eysenhardtii, Gegenbaur.

Rhizophysa filiformis, Huxley, T. H., 1859, Oceanic Hydrozoa, p. 90, Pl. VIII. Figs. 13–20.

Rhizophysa Eysenhardtii, Gegenbaur, C., 1859, Nova Acta Acad. Nat. Curios., Tom. 27, p. 408, Taf. 31, Fig. 46–49.

Nectophysa Wyvillei, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 327, Pl. XXIII. Figs. 1–8.

This Siphonophore is found occasionally at the Tortugas, Florida. It has been obtained by Haeckel in the Canary Islands, by the Plankton Expedition in the Sargasso Sea, and by Fewkes in the Bermudas.

Rhizophysa clavigera, Chun.

Cannophysa filiformis, Mayer, A. G., 1894, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXV. p. 241, Pl. III. Fig. 3.

Rhizophysa clavigera, Chun, C., 1897, Siphonophoren der Plankton Expedition, p. 104.

A single specimen of this Siphonophore was found floating within ten metres of the surface in the Gulf Stream between Havana and Key West.

PHYSALIA, Bosc, 1802.

Physalia pelagica, Bosc.

Salacia phisalus, Linné, 1756, Systema Naturæ, p. 158.

Holothuria physalis, Linné, 1767, Syst. Naturæ, Ed. XII. p. 1090.

Medusa caravella, Müller, O. F., 1776, Besch. Berlin Gesell. Natur. Freunde, Bd. II. p. 290, Taf. IX. Fig. 1.

Arethusa crista subrubella venosa, Browne, P., 1789, Nat. Hist. Jamaica, p. 386.

Physalia pelagica, Bosc, L. A. G., 1802, Hist. Nat. d. Vers., Tom. II. p. 168.

Physalis arethusa, Tilesius, W. G., 1812, Krusenst. Reise, p. 91, Pl. XXIII. Figs. 1–6.

Physalia caravella, Eschscholtz, F., 1829, Syst. der Acalephen, p. 160, Taf. XIV.

Physalia aurigera, McCrady, J., 1857, Gymn. Charleston Harbor, p. 74.

Physalia Olfersii, Quatrefages, A. de, 1854; Ann. des Sci. Nat., Ser. 4, Zoöl., Tom. II. p. 112, Pl. III. Figs. 1–9; Pl. IV. Figs. 1, 2.

Caravella maxima, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. pp. 313, 338, 352, Pl. XXVI. Fig. 8.

Physalia maxima, Goto, S., 1897, Journ. Coll. Sci. Imperial Univ., Tōkyō, Japan, Vol. X. Part II. p. 175, Taf. XV. Figs. 1–12.

This large Siphonophore is frequently seen throughout the year floating past the Islands of the Tortugas, Florida, and a southerly breeze is almost sure to strand large numbers of them upon the beaches. The animal is found all over the Tropical and Subtropical Atlantic. It is carried by the Gulf Stream to the shore of Europe, and is often found in the Mediterranean near the Straits of Gibraltar. It appears, however, not to be permanently established in the Mediterranean. During the latter part of the summer this Siphonophore is quite common along the southern coast of New England, and individuals have been found as far north as the Bay of Fundy.

SPHÆRONECTES, Huxley, 1859.

Sphæronectes gracilis, Haeckel.

Fig. 89, Plate 27.

Monophyes gracilis, Claus, C., 1874, Schrift. Zoöl. Inst. Wien, II. Die Gattung Monophyes, p. 29, Taf. IV. Figs. 8–14.

Sphæronectes inermis, Fewkes, J. W., 1880, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. VI. p. 143, Pl. II. Fig. 6.

This Siphonophore is abundant in the Mediterranean and Tropical Atlantic. It was found throughout the winter by Chun in the Canary Islands, and several specimens were found by us at the Tortugas, Florida, in July, 1898. A single specimen of its sexual generation (Diplophysa inermis) was found by Fewkes (1881; Bull. Mus. Comp. Zoöl., Vol. VIII. p. 166, Plate VI. Figure 12), in Newport Harbor, Rhode Island.

The Atlantic species of Sphæronectes is closely allied to, if not identical with, S. Köllikeri of the Tropical Pacific. Chun (1892, Abhandl. Senck. Gesell., Bd. 18, p. 86) says that in S. Köllikeri the distal portion of the phyllocyst curves downward toward the edge of the swimming-bell, while in S. gracilis it bends upwards. Our observations on S. Köllikeri from the Fiji Islands do not support this view (see Agassiz and Mayer, 1899 Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 177, Plate 16, Figure 51), for there appears to be much individual variability in respect to the curvature of the phyllocyst in the Pacific species. All of the specimens of S. gracilis observed in the Tortugas, Florida, were colorless, whereas S. Köllikeri is often quite highly colored; the entoderm of the feeding-polypites being bright yellow, and the nematocyst batteries of the tentacles orange.

DIPHYES, Cuvier, 1817.
EUDOXIA, Eschscholtz, 1825.

Diphyes bipartita, Costa.
Eudoxia campanula, Leuckart.

Figs. 114, 114^a, Plate 34.

Polygastric Generation

- Diphyes bipartita, Costa, O. G., 1840, Genere Diphya, p. 4, Taf. IV.
- Diphyes acuminata, Leuckart, R., 1853; Die Siphonophoren, p. 61, Taf. III. Figs. 11–19.
- Diphyes gracilis, Gegenbaur, C., 1854, Zeit. für Wissen. Zoöl., Bd. V. p. 309, Taf. XVI. Figs. 5–7.
- Diphyes Sieboldii, Kölliker, A., 1853, Die Schwimmpolypen der Messina, p. 36, Taf. XI. Figs. 1–8.

This species is very abundant all over the Tropical Atlantic and in the Mediterranean; and specimens are often found at Newport, Rhode Island, late in the summer.

DIPHYOPSIS, Haeckel, 1888.
ERSÆA, Eschscholtz, 1829.

Diphyopsis campanulifera, Chun.

Figs. 93-95, Plate 28.

Polygastric Generation

Diphyes ——, Quoy, J. R. C., and Gaimard, P., 1827, Ann. des Sci. Nat., Tom. 10, Pl. I. Fig. 7.
Diphyes campanulifera, Eschscholtz, F., 1829, Syst. der Acalephen, p. 137.
Diphyes Bory, Quoy, J. R. C., and Gaimard, P., 1833, Voyage de l'Astrolabe, Tom. IV. Zoöphytes, p. 83, Pl. IV. Figs. 1-6.
Diphyopsis campanulifera, Chun, C., 1888, Sitzungsber. Akad. Wissen. Zoöl., Bd. XLIV. p. 1159.
Diphyopsis compressa, Haeckel, E., 1888, Siphonophoræ., Challenger Report, Zoöl., Vol. XXVIII. p. 153, Plates 33, 34, 18 Figs.

Ersæa Lessonii, Chun.

Figs. 96, 97, Plate 28.

Free Sexual Generation

Ersæa Gaimardi, Eschscholtz, F., 1829, Syst. der Acalephen, p. 128, Taf. XII. Fig. 4.
Eudoxia Lessonii, Huxley, T. H., 1859, Oceanic Hydrozoa, p. 57, Pl. III. Fig. 6.
Ersæa compressa, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 123, Pl. XXXIV. Figs. 9-18.

This Siphonophore is common all over the Tropical and Subtropical Atlantic. A few individuals are drifted into Newport Harbor every summer by the southerly winds, and are probably blown northward from the waters of the Gulf Stream.

Diphyopsis picta.

Polygastric Generation

Doramasia picta, Chun, C., 1888, Sitzungsber. Akad. Wissen. Berlin, Bd. XLIV. p. 1154.
Doramasia picta, Chun, C., 1892, Abhandl. Senckenberg Gesell., Bd. XVIII. p. 91, Taf. VIII. Fig. 3; Taf. IX. Figs. 5-9.

Ersæa picta, Chun.

Fig. 118, Plate 34.

Free Sexual Generation

Ersæa picta, Chun, C., 1888, Sitzungsber. Akad. Wissen. Berlin, Bd. XLIV. p. 1154.

This form has been found by Chun in the Canary Islands, and it is also common at the Tortugas, Florida. We present a figure of the free sexual generation.

{ Diphyopsis hispaniana,[1] nov. sp.
{ Ersæa hispaniana, nov. sp.

Figs. 98–99, Plate 29.

Polygastric generation = Diphyopsis hispaniana.
Monogastric, sexual generation = Ersæa hispaniana.

Specific Characters. — Diphyopsis hispaniana. Figures 98, 99. The animal is 12 mm. in length. The cavity of the anterior swimming-bell is very voluminous, so that the bell walls are remarkably thin. They are, however, quite rigid, so that swimming is accomplished almost entirely by the movements of the powerful velum. There is a well-developed hydrœcium upon the ventral side of the anterior swimming-bell, and a long spindle-shaped phyllocyst arises from its inner apex, and extends upwards along the side of the bell cavity. The siphosome arises from the inner apex of the hydrœcium, immediately under the point of origin of the phyllocyst. The first appendage of the siphosome is the large posterior swimming-bell that is almost as large as the anterior. It is provided with 4 radial canals, and a circular vessel, and these are placed in connection with the gastro-vascular space of the siphosome by means of a long slender duct. The posterior swimming-bell possesses a well-developed velum, the contractions of which acting simultaneously with those of the velum of the anterior swimming-bell, cause the animal to dart through the water at a very rapid rate. The posterior swimming-bell is provided with two large lateral wings having serrated edges. The siphosome extends downward through the groove between these wings. The order of development of the various organs upon the siphosome is as follows: — First the feeding-polypites, then the tentacles, then the gonads and swimming-bells, and lastly the covering scales. The feeding-polypites are spindle-shaped, and quite contractile. The outer surface of their proximal portions displays a number of wart-like swellings. The entodermal cells of these swellings are of a decided ochre-yellow color, and it seems not improbable that their function may be similar to that of the "liver cells" of the feeding-polypites of Agalma. The tentacles arise from the sides of the feeding-polypites very near their point of origin from the siphosome. They give rise to a number of lateral branches that are studded with sharply projecting nematocyst cells. (See Figure 99.) These lateral branches terminate in swollen nematocyst batteries. The covering scales are spathiform and possess a deep ventral groove. A single gonad and a swimming-bell bud out side by side, very close together, from the base of each feeding-polypite.

When sufficiently developed, each unit, consisting in a feeding-polypite, tentacle, gonophore, swimming-bell and covering scale, is set free from the siphosome of Diphyopsis hispaniana, and becomes the free-swimming, monogastric, sexual generation known as Ersæa hispaniana.

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[1] Called "hispaniana" on account of its red and yellow coloration. The entoderm of the feeding-polypites being ochre-yellow, and the tentacular nematocyst-batteries port-wine-red.

Ersæa hispaniana, nov. sp.

Fig. 100, Plate 29.

Specific Characters. — Ersæa hispaniana. The mature animal is 7 mm. in length. The covering scale is hood-shaped without a sharp apex. Its lower portion is sharp-edged, and overlaps the large swimming-bell. The phyllocyst is short and blunt, and contains a highly refractive "oil" globule. The large swimming-bell is provided with 4 longitudinal, serrated ridges that give it a rectangular appearance in cross-section. There are 4 radial tubes, a circular vessel, and a well-developed velum. Two or more gonophores are seen budding out from the side of the feeding-polypite near its base. These gonophores (*g*, Figure 100) are medusiform and are provided with 4 radial tubes, a circular vessel, and a velum. The genital products are found within the manubrium. In Figure 100 a single large, oval egg is seen occupying this position.

Both Diphyopsis hispaniana and Ersæa hispaniana were common at the Tortugas, Florida, in July, 1898, but were not seen during the summer of 1899.

ABYLA, Quoy and Gaimard, 1827.
AGLAISMA, Eschscholtz, 1829.

Abyla pentagona, Eschscholtz.

Figs. 101, 101^{a}–103, Plate 30.

Polygastric Generation

Abyla pentagona, Eschscholtz, F., 1829, Syst. der Acalephen, p. 132.

Calpe pentagona, Quoy, J. R. C., and Gaimard, P., 1827, Ann. der Sci. Nat., Tom. X. p. 11, Pl. 2 A. Figs. 1–7.

Abyla trigona, Vogt, C., 1854, Mém. de l'Institut Nat. Génevois, Tom. I. p. 121, Pl. XX. Figs. 4–7; Pl. XXI. Figs. 3–6, 10–13.

Calpe Gegenbauri, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 164, Pl. XXXIX. Figs. 1–12.

Abylopsis pentagona, Chun, C., 1897, Siphonophoren der Plankton Expedition, Bd. II. K. b. p. 30.

Aglaisma cuboides, Chun.

Fig. 104, Plate 30.

Free Sexual Generation

Eudoxia cuboides, Leuckart, R., 1853, Siphonophoren, p. 59, Taf. III. Figs. 7, 8, 10.

Einzelthiere der Abyla pentagona, Gegenbaur, C., 1854, Zeit. für Wissen. Zool., Bd. V. p. 295, Taf. XVI. Figs. 1, 2.

Aglaisma Gegenbauri, Haeckel, E., 1888, Siphonophoræ, Challenger Report, Zoöl., Vol. XXVIII. p. 119, Plate XL. Figs. 13–20.

Aglaisma cuboides, Chun, C., 1897, Siphonophoren der Plankton Expedition, p. 30.

This form is quite common at the Tortugas, Florida, as indeed it is all over the Tropical and Subtropical Atlantic. It is found in Charleston Harbor, South Carolina, but has not yet been taken north of the Carolina coast.

Abyla quincunx, CHUN.

Figs. 115–117, Plate 34.

Polygastric Generation	Abyla pentagona, Huxley, T. H., 1859, Oceanic Hydrozoa, p. 40, Pl. II. Figs. 2–2^e. Abylopsis quincunx, Chun, C., 1888, Sitzungsber. Akad. Wissen. Berlin, Bd. XLIV. p. 1160.

Aglaisma quincunx.

Free Sexual Generation	Aglaismoides Eschscholtzii, Chun, C., 1888, Sitzungsber. Akad. Wissen. Berlin, Bd. XLIV. p. 1160. Aglaismoides quincunx, Chun, C., 1897, Siphonophoren der Plankton Expedition, p. 29.

Chun found this Siphonophore in the Canary Islands, and it was taken by the Plankton Expedition in the Gulf Stream and Sargasso Sea. Huxley, 1859, found it in the tropical regions of the Atlantic, Pacific, and Indian Oceans. It has been taken by Agassiz and Mayer (1899; Bull. Mus. Com. Zoöl., Vol. XXXII. p. 180) in the Fiji Islands. These South Pacific specimens are, however, slightly different from those of the Atlantic in that their tentacular nematocyst-batteries are usually colorless instead of more or less orange, as in the Atlantic form.

Chunia capillaria, nov. gen. et sp.

Figure 90, Plate 27.

Generic Characters. — Chunia, novum genus. This genus belongs to the family Diphyidæ, Eschscholtz, and to the subfamily Abylinæ, L. Agassiz. It possesses a pentagonal, prismatic, anterior swimming-bell and a larger five-sided, posterior swimming-bell. The siphosome bears a long, slightly curved, sharp-pointed, hair-like bristle. The covering scales, or bracts, are leaf-shaped. The monogastric sexual generation is unknown.

Specific Characters. — The animal is about 10 mm. in length. The anterior swimming-bell is prismatic, and possesses one oblique, five-sided face and 5 lateral faces. Four of these are plane, but the fifth is sharply concave. The cavity of the swimming-bell opens upon this concave face. The bell cavity is long and spindle-shaped, and is provided with 4 radial tubes and a velum. There is a large spherical phyllocyst that gives rise to an apical cæcum containing a highly refractive "oil" globule. The hydrœcium of the anterior swimming-bell is long and tube-like, and its axis is parallel to that of the bell cavity. Indeed, it is quite similar in form to the hydrœcium of Abyla quincunx (see Figure 115, Plate **34**). The first appendage of the siphosome is the posterior swimming-bell. This is somewhat larger than the anterior and is five-sided, the sides being bounded by prominent, angular, serrated ridges. There is a single median dorsal ridge and two pairs of lateral ridges. The ventral-most pair of lateral ridges are wing-like, and enclose a trough-like groove through which the siphosome extends. The bell cavity of the posterior swimming-bell is spindle-shaped and is provided with 4 radial tubes and a circular vessel. These are placed in communication with the general gastro-vascular cavity of the siphosome by means of a long slender duct. The posterior swimming-bell is furnished with a powerful velum, by the contractions of which the animal is enabled to shoot through the water. The siphosome is not very long and rarely extends beyond the posterior extremity of the trough-like groove in which it lies. The first organs to be developed upon it are the feeding-polypites; the tentacles soon arise as buds from the sides of the polypites, each feeding-polypite being provided with a single tentacle. The tentacles give rise to lateral branches each one of which terminates in a swollen cylinder-shaped nematocyst battery.

A long, slightly curved, bristle-like spine arises from the siphosome at a short distance below its origin, and extends outward to a considerable distance beyond the distal end of the posterior swimming-bell. It seems probable that this structure may be morphologically equivalent to a bract, that has become thus modified for defensive purposes. Other covering scales or bracts were observed upon the siphosome, but these were leaf-shaped (see *c s*, Figure 90, Plate **27**). No gonophores or sexual organs were observed, and the sexual generation is unknown.

This rare form is found among the Bahama Islands during the winter months. The specimen from which we have obtained our figure was captured in Nassau Harbor, New Providence Island. We also obtained a specimen at Watlings Island (San Salvador) on January 15, 1893.

AGALMA, Eschscholtz, 1825.

Agalma Pourtalesii, Agassiz and Mayer.

Figures 106-113, Plates 31-33.

Agalma Pourtalesii, Agassiz, A., and Mayer, A. G., 1899; Acalephs from the Fiji Islands, Bull. Mus. Comp. Zoöl. at Harvard Coll., Vol. XXXII. p. 180.

Specific Characters. — The entire animal (Plate **32**) is about 25 mm. in length. The feeding-polypites, dactylozoids, tentacles, and gonostyles, all arise from the ventral side of the siphosome. The float, or pneumatophore, is of small size, and its apical pore is surrounded by radially arranged streaks of dark red pigment. The swimming-bells (Figures 109, 110, Plate **33**) are dovetailed alternately, one above another, so that their velar openings are situated on two diametrically opposite sides of the nectosome (see Figure 108).

The siphosome is densely covered upon all sides with thick prismatic bracts, or covering scales. One of these bracts detached from the animal is shown in Figure 112. The angular edges of the older bracts are usually smooth, but in the younger ones they frequently display a row of regularly arranged nematocyst-bearing papillæ (see Figure 113). A single, long, slender canal runs through the substance of each bract.

The feeding-polypites are somewhat stouter in shape than the dactylozoids, but in other respects are quite similar to them in appearance. They are quite contractile, and their mouths may be expanded, at will, so as to assume a funnel shape.

The tentacles arise from the bases of the dactylozoids and feeding-polypites. Each tentacle gives off a number of lateral branches, each one of which terminates in a coiled nematocyst-battery, an ampulla, and two paired finger-like processes (see Figure 111, Plate **33**).

Both male and female gonostyles spring from the siphosome of the same individual. They arise from the ventral side of the siphosome between the dactylozoids and feeding-polypites (see Figure 108). The gonophores arise from the sides of the gonostyles. The male gonophores are long and slender, while the female are short and stout. Both resemble medusa buds and are provided with 4 radial tubes, a circular vessel, and a velum. The genital products occupy the manubrium. The gonophores are borne upon long slender filaments attached to the sides of the gonostyle. These filaments are highly contractile.

The color of the entoderm of the stem, swimming-bells, feeding-polypites, and dactylozoids is rose-pink. The nematocyst batteries upon the terminal portions of the tentacles are port-wine-red. The gonads and bracts are colorless.

This species was found by us at the Tortugas Islands in June, 1897. We also met with it in Suva Harbor, Fiji Islands, in December, 1898.

Agalma virida, nov. sp.

Figs. 119-121, Plate 35.

A single immature individual of this beautiful species was obtained on June 6, 1899, at the Tortugas.

Specific Characters.— The animal is 3 mm. in length. The float is spherical and almost egg-shaped, and is covered by one of the larval bracts. The pore is a simple round opening at the aboral pole of the float, and is surrounded by large, polygonal pigment cells. There is a single large axial feeding-polypite which is capable of much expansion and contraction. The gastric cells of this polypite are large and oval. Six to eight mouthless cystons arise from the side of the feeding-polypite. These are stiff and slender, and their distal extremities are armed each with several oval nematocyst cells of large size. The entoderm of the cystons display large, highly refractive oval cells quite similar to the digestive cells of the feeding-polypite. About half a dozen branched tentacles arise from between the cystons. Each branch terminates in a complexly formed coiled nematocyst battery which is enclosed within the substance of the terminal knob. The knob ends distally in a bladder-shaped ampulla and a pair of long curved finger-shaped processes, the latter being lined on their convex sides with a row of hair-cells (see Figure 120). Several small hernia-like protuberances, which probably consist of young swimming-bells, arise from the side of the main axis immediately below the level of the float. The bracts are three-cornered, and their sharp distal ends are armed with large nematocyst cells. The free edges of the primitive larval bract are lined with a row of small nematocyst cells. Each bract is provided with a long slender, unbranched canal. The pigment cells of the float are rich brown in color. The entoderm of the feeding-polypite and cystons is of a decided pink, and the coiled nematocyst batteries in the tentacle knobs are of a more decided reddish color. The entoderm of the float and the ectoderm of the terminal knobs of the tentacles are yellow, and the canals of the bracts are grass-green in color.

IV. CTENOPHORÆ.

OCYRÖE, Rang, 1826.

Ocyroë crystallina, Rang.

Fig. 105, Plate 31.

Ocyroë crystallina, Rang, S., 1828, Mem. Soc. Nat. Paris, Tom. IV. p. 172, Pl. XX. Fig. 4.

This Ctenophore is quite often met with at the Tortugas, Florida, from April until July. It makes its appearance at the surface when the ocean is perfectly flat and calm, and even a slight ripple is sufficient to induce it to sink into the depths. The species appears to be widely distributed over the Tropical Atlantic.

BOLINA, Mertens, 1833.

Bolina vitrea, L. Agassiz.

Figs. 91, 92, Plate 27.

Bolina vitrea, Agassiz, L., 1860, Cont. Nat. Hist. U. S., Vol. III. pp. 269, 289, Fig. 93.

Bolina littoralis ? McCrady, J., 1858, Proc. Elliott Soc., Charleston, p. 1, Pl. 14.

Large numbers of this Ctenophore may be seen floating in the water on almost any calm day throughout the summer at the Tortugas, Florida. It is also common among the Florida Reefs, and probably extends as far up the coast as Charleston, South Carolina.

HORMIPHORA, Agassiz, L., 1860.

Hormiphora plumosa? Chun.

Cydippe hormiphora, Gegenbaur, C., 1856; Archiv für Naturges., p. 200, Taf. VIII. Fig. 10.

Hormiphora plumosa, Chun, C., 1880, Die Ctenophoren des Golfes von Neapel, p. 281, Taf. I. Figs. 5, 6; Taf. II. Figs. 2, 3; Taf. III. Figs. 8, 9.

Numerous fragments of a Hormiphora, that may be specifically identical with the common H. plumosa of the Mediterranean, were found during the summer of 1898 at the Tortugas, Florida.

Unfortunately no perfect specimens were captured, and we must remain in doubt concerning the specific identity of this animal with H. plumosa.

EUCHARIS, Eschscholtz, 1825.

Eucharis multicornis? Eschscholtz.

Eucharis multicornis, Eschscholtz, F., 1829, Syst. der Acalephen, p. 31.

A species of Eucharis believed to be specifically identical with E. multicornis of the Mediterranean is found at Key West and the Tortugas, Florida.

BERÖE, Browne, 1789.

Beroë Clarkii.

Beroë, Browne, P., 1789, The Civil and Nat. Hist. of Jamaica, p. 384, Table 43, Fig. 2.

Idyiopsis Clarkii, Agassiz, L., 1860, Cont. Nat. Hist. U. S., Vol. III. pp. 288, 296; Figs. 101, 102.

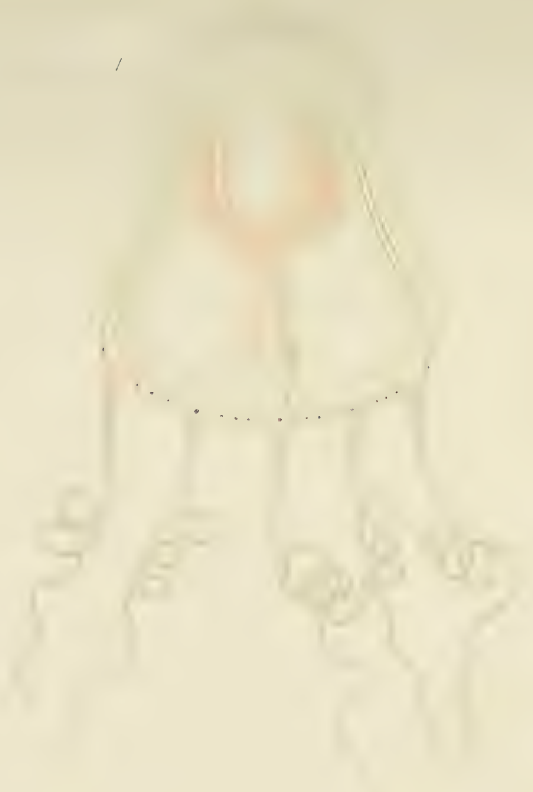
This Ctenophore is very abundant among the Bahama, Tortugas, and Florida Reefs; and it extends as far northward as Charleston Harbor, South Carolina.

PLATE 1.

Fig. 1. Pandea violacea, Agassiz and Mayer.
Fig. 2. Stomotoca australis, nov. sp.

PLATE I.

1



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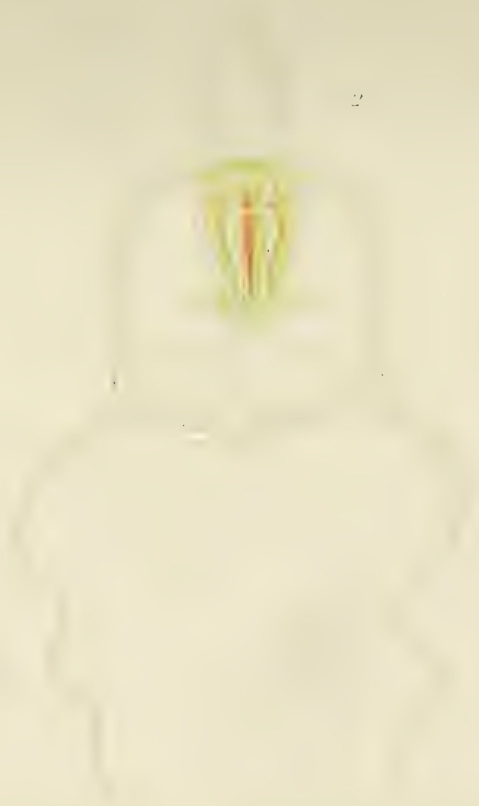
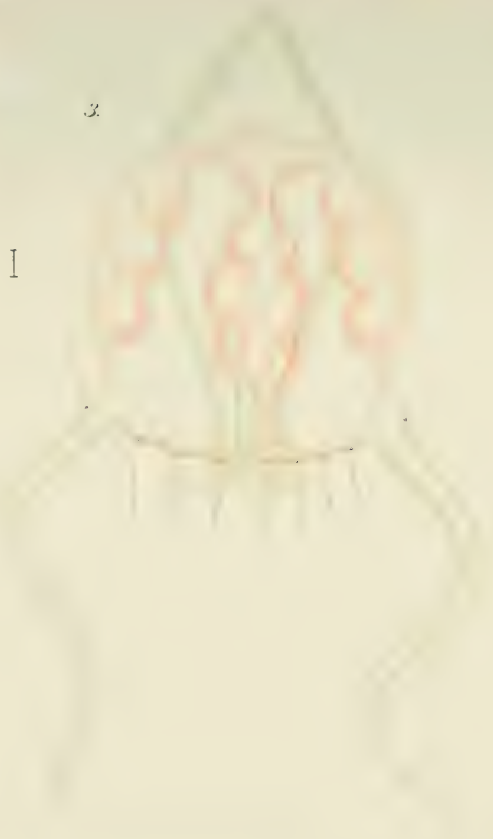


B. Meisel lith Boston.

PLATE 2.

Fig. 3.	Dissonema turrida, nov. sp.	Adult medusa.
Fig. 4.	" " "	Young medusa.

3.



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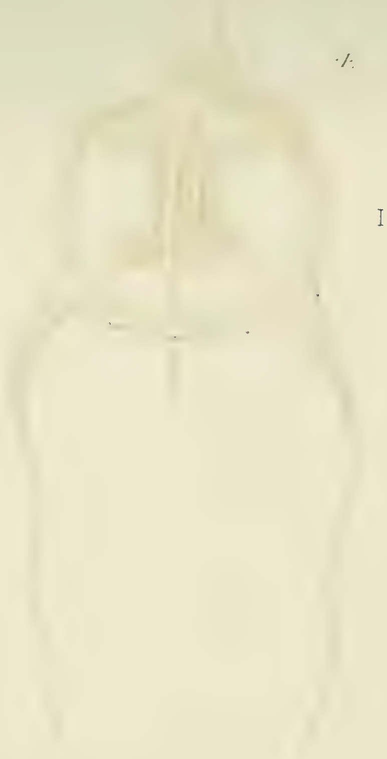
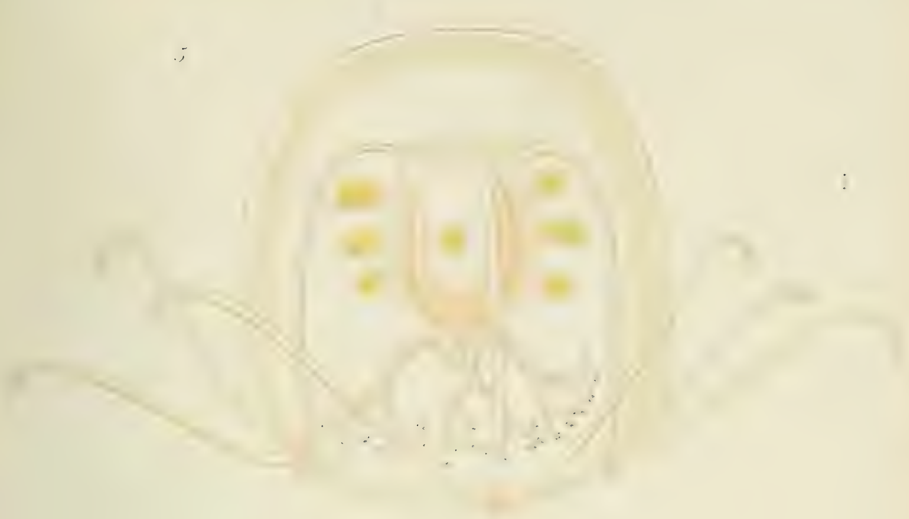


PLATE 3.

Fig. 5. Bougainvillia frondosa, nov. sp.
Fig. 6. Gonionemoides geophila, nov. gen. et sp. Portion of bell margin showing sucker-bearing and nematocyst-bearing tentacles.
Fig. 7. Gonionemoides geophila, otocyst.

5



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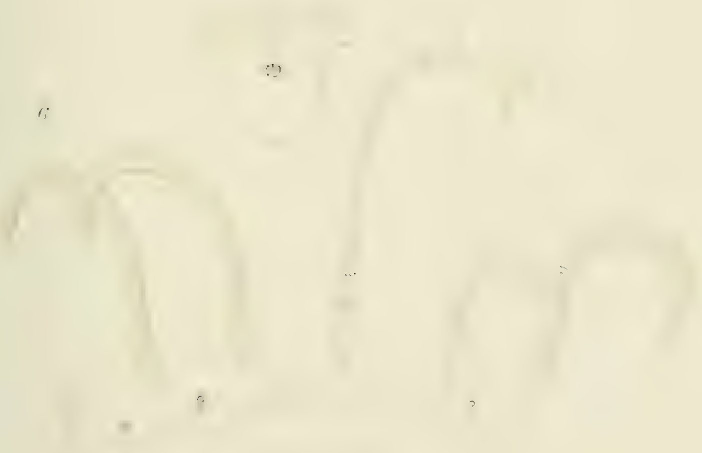


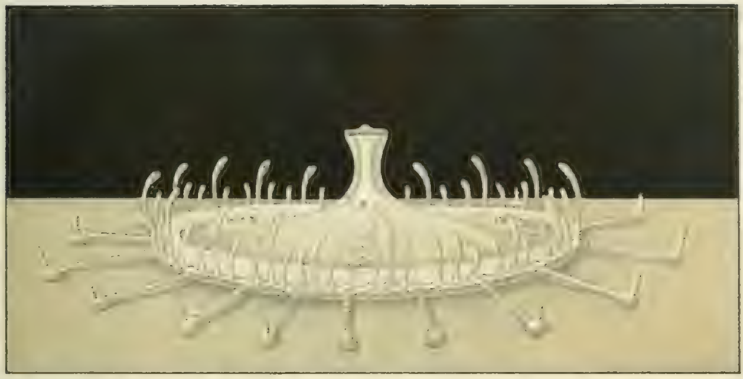
E. Meisel, lith. Boston

PLATE 4.

Fig. 8. Gonionemoides geophila, nov. gen. et sp. Side view of adult medusa.

Fig. 9. " " Medusa with oral surface upward, and holding fast to the bottom of the aquarium by means of the adhesive suckers upon its tentacles.

9



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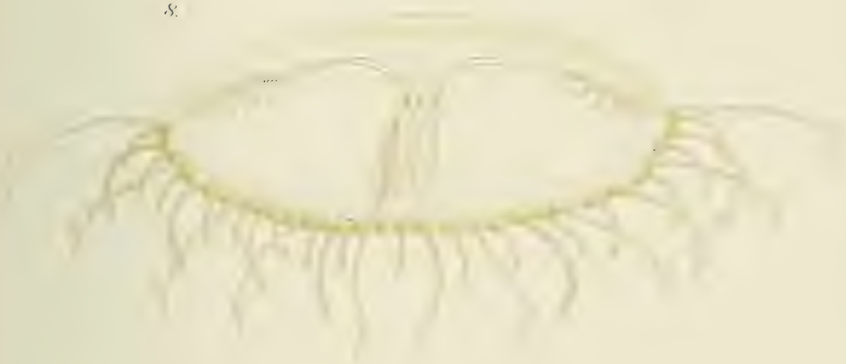
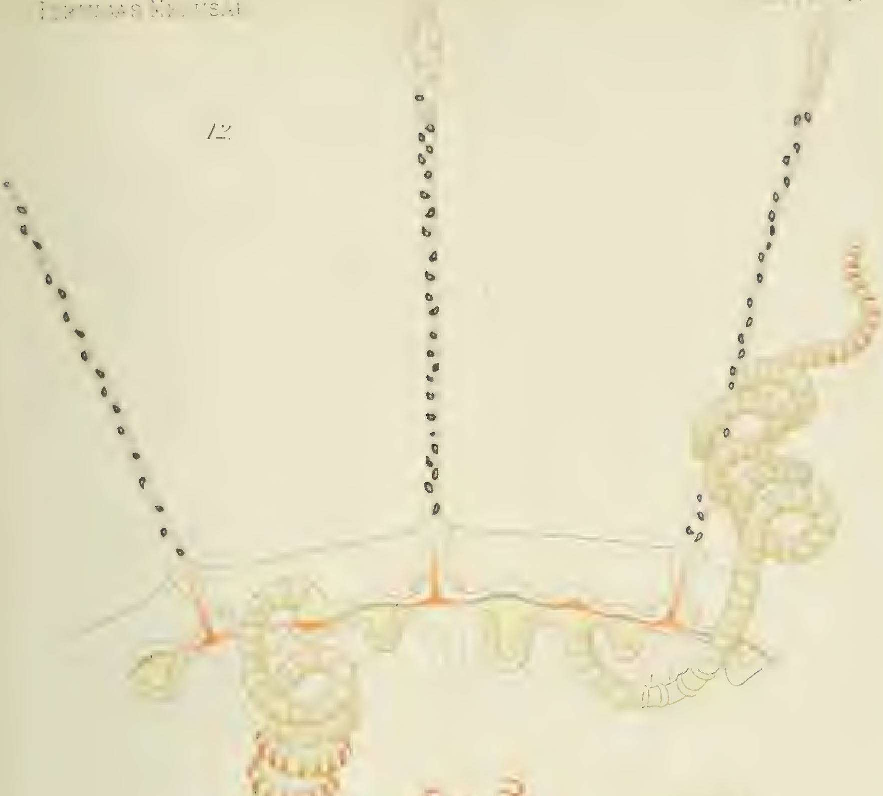


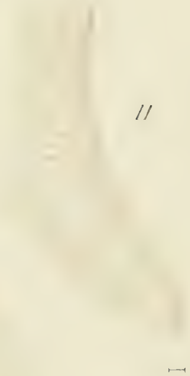
PLATE 5.

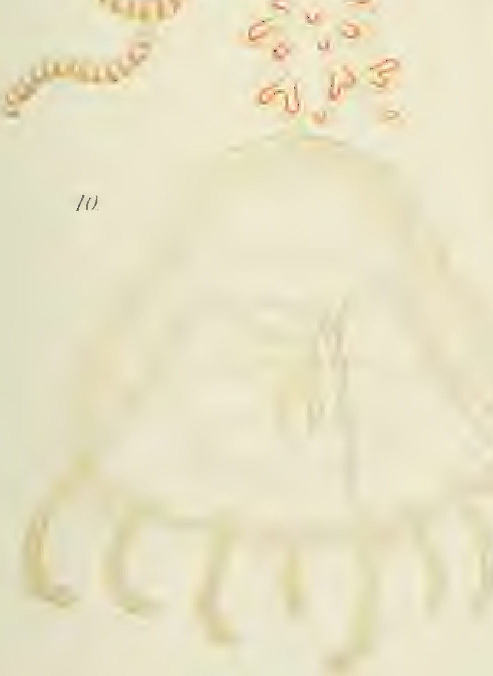
Fig. 10. Gonionemoides geophila, nov. sp. Young medusa.

Fig. 11. Gonionemoides geophila, nov. sp. Distal end of tentacle showing the beginning of the formation of the suctorial disk.

Fig. 12. Halicalyx tenuis, Fewkes. Portion of bell margin.



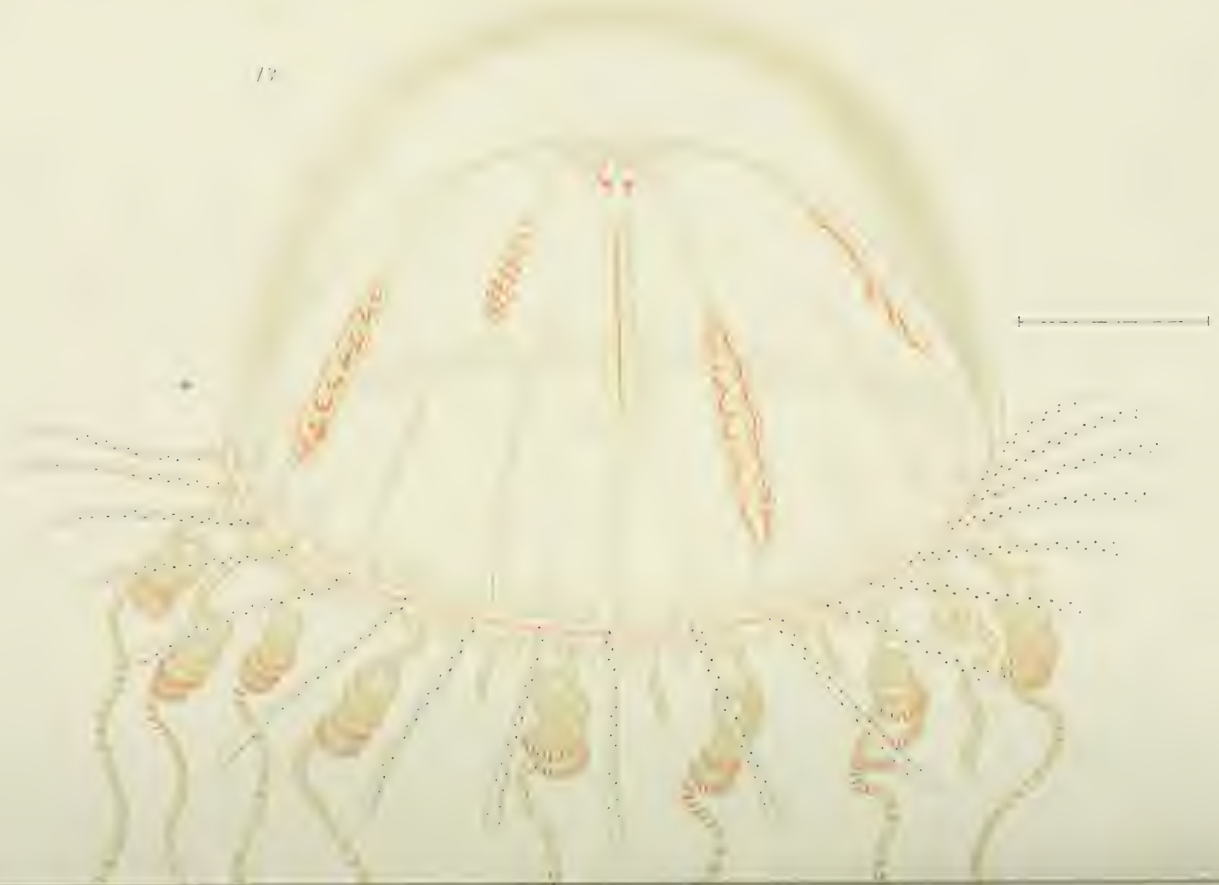




B. Meisel lith. Boston

PLATE 6.

Fig. 13. Halicalyx tenuis, Fewkes. Side view of mature medusa.



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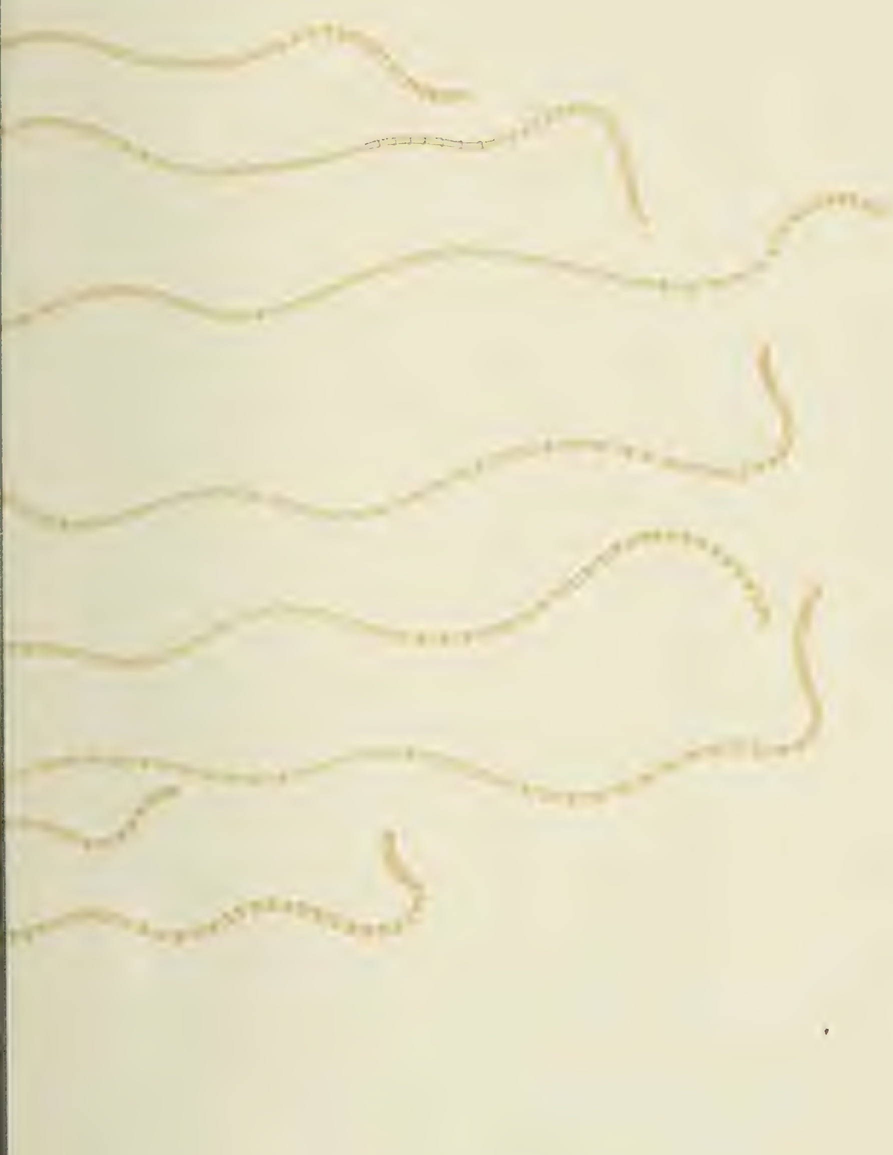


A. G. M. del.

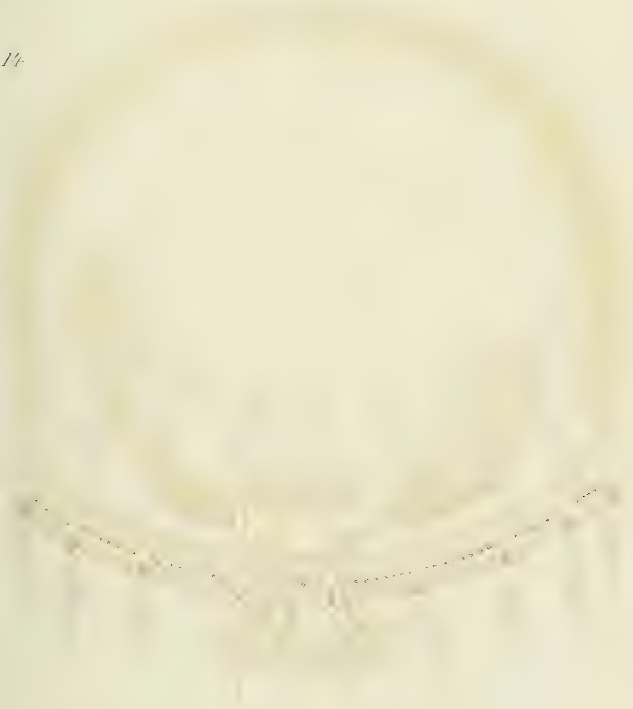
B. Meisel lith Boston.

PLATE 7.

Fig. 14. Tetracannota collapsa, nov. gen. et sp. Adult medusa.
Fig. 15. " " " " Very young medusa.

15

14

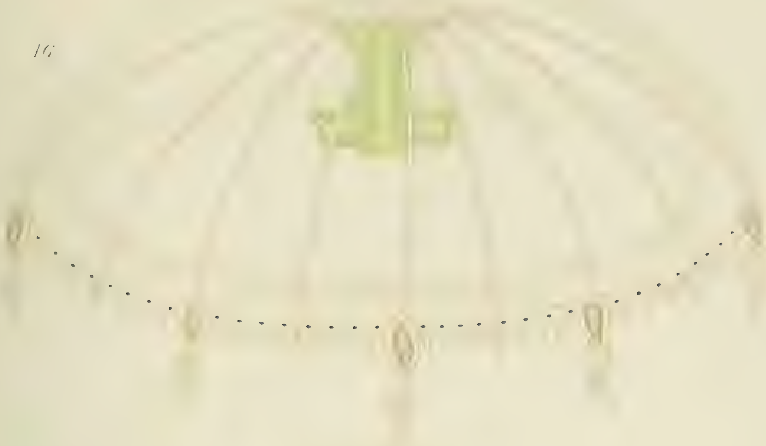


B Meisel lith Boston.

PLATE 8.

Fig. 16. Tetracannota collapsa, nov. gen. et sp Half-grown medusa.
Fig. 17. Dyscannota gemmifera = Willia gemmifera, Fewkes.

16



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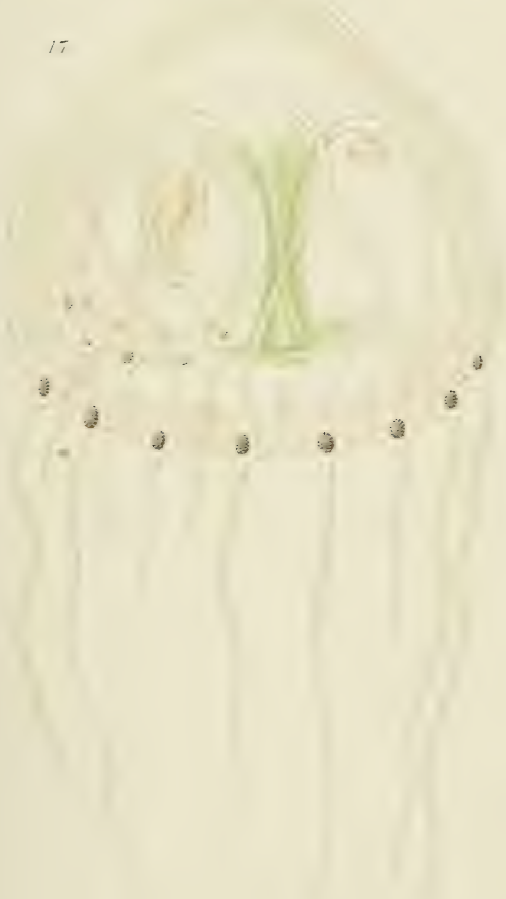


[illegible]

B Meisel lith Boston

PLATE 9.

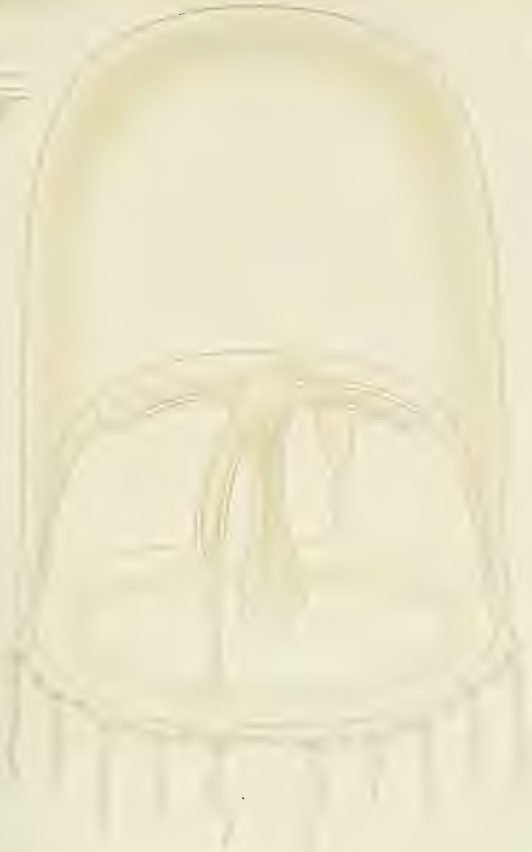
Fig. 18. Oceania magnifica, nov. sp.
Fig. 18ª. " " Portion of bell margin, showing otocysts.
Fig. 19. Oceania globosa, nov. sp.
Fig. 19ª. " " Portion of bell margin.

PLATE 10.

Fig. 20. Oceania gelatinosa, nov. sp.
Fig. 20^{a}. " " Otocyst.
Fig. 21. Phortis pyramidalis = Eutima pyramidalis, L. Agassiz.
Fig. 21^{a}. " " Portion of bell margin.

20a

20



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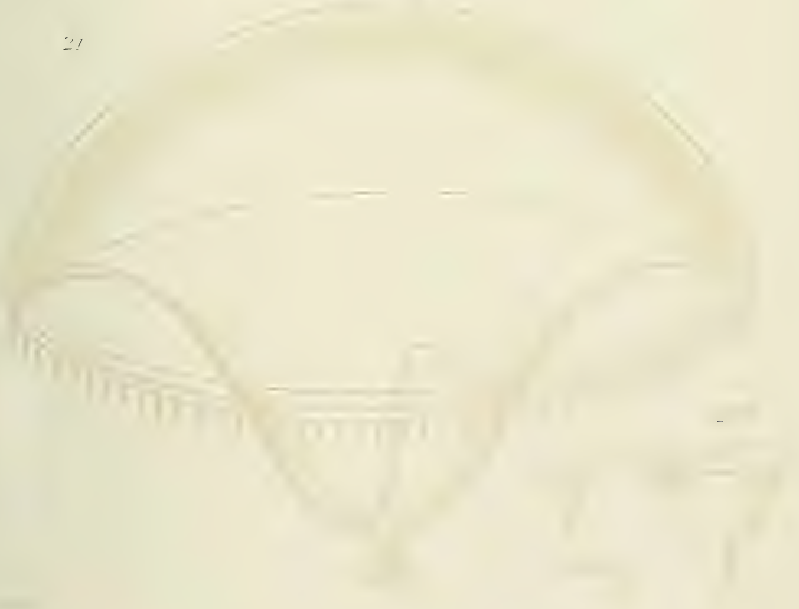


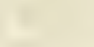
PLATE 11.

Fig. 22. Eutimalphes cœrulea = Eirene cœrulea, L. Agassiz.
Fig. 22^{a}. " " Portion of bell margin.
Fig. 23. Zygodactyla cyanea, L. Agassiz. Young medusa.
Fig. 23^{a}. " " Otocysts.

22a
22
23
23a

PLATE 12.

Fig. 24. Pseudoclytia pentata, nov. gen. et sp. Side view.
Fig. 25. " " Oral view of medusa.
Fig. 26. " " Side view of otocyst.



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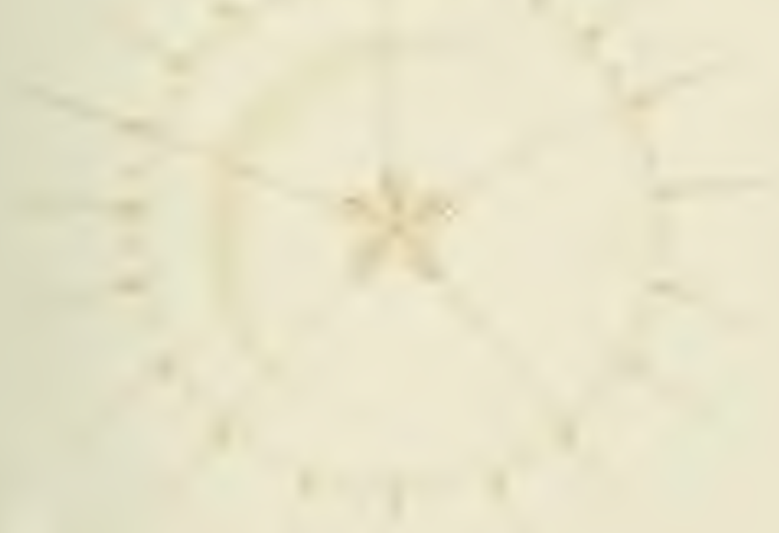


PLATE 13.

Fig. 27. Rhacostoma dispar, nov. sp. Side view of medusa.
Fig. 28. " " Oral view of medusa.
Fig. 29. " " Otocyst.

27

29

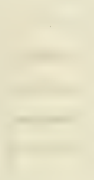
28

B. Meisel lith. Boston

PLATE 14.

Fig. 30. Æginella dissonema, Haeckel. Side view of medusa.
Fig. 31. " " Longitudinal section of tentacle.
Fig. 32. " " Marginal sense-organ.

31.



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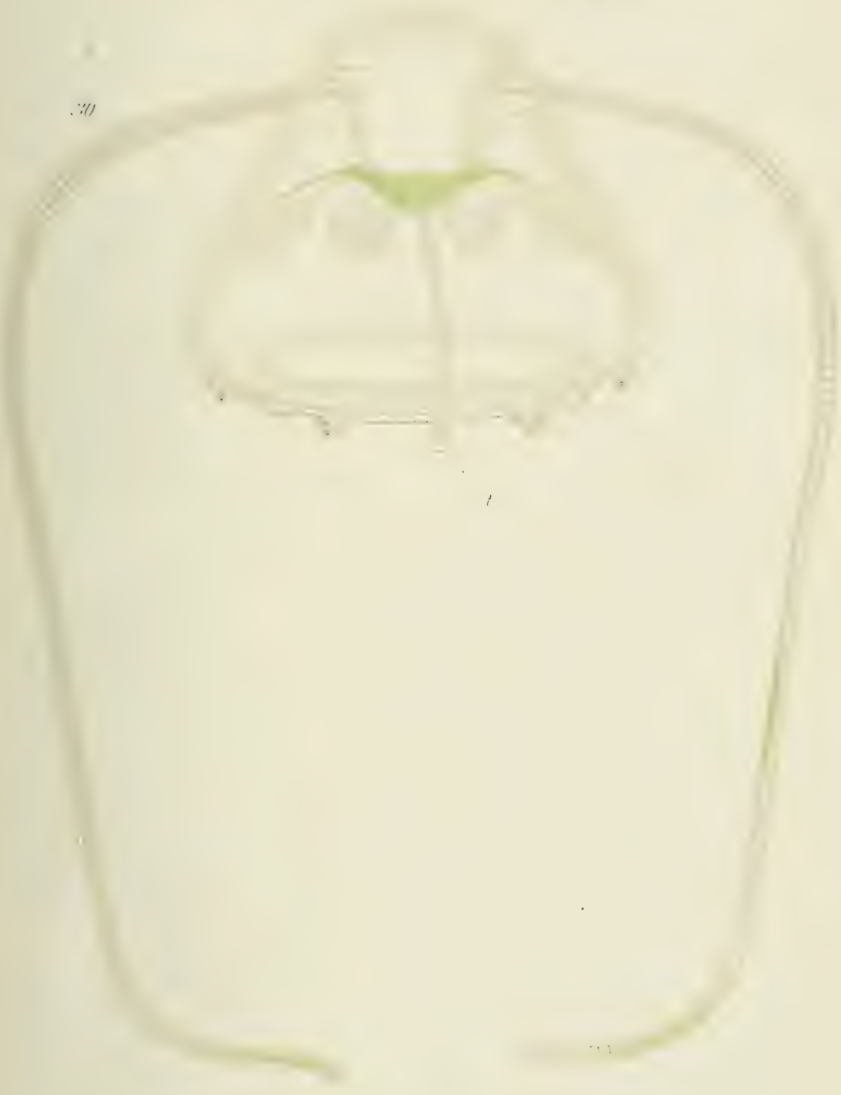
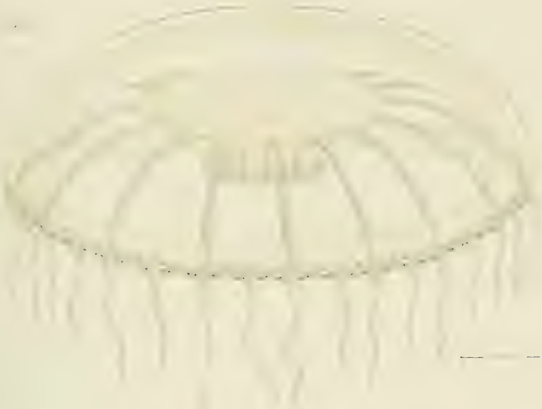
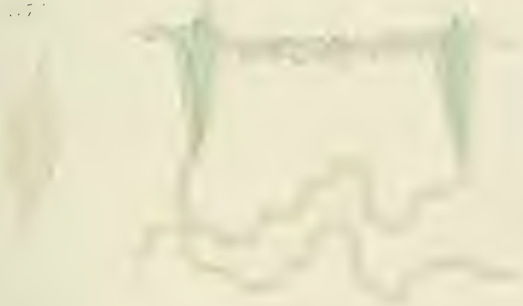


B Meisel lith Boston

PLATE 15.

Fig. 33. Zygodactyla cyanea, L. Agassiz. Medusa with 16 radial tubes.
Fig. 34. " " Portion of bell margin.
Fig. 35. Pseudoclytia pentata, nov. gen. et sp., red variety.
Fig. 35^{a}. " " View of ovary.





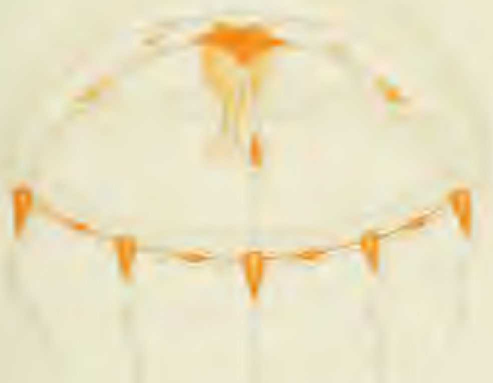


PLATE 16.

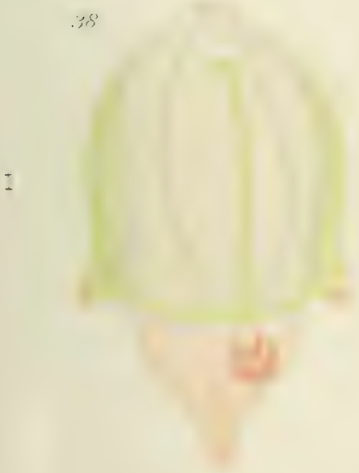
Fig. 36. Steenstrupia gracilis, Brooks. Mature medusa ♂.
Fig. 37. " " Young medusa.
Fig. 38. Ectopleura minerva, nov. sp.
Fig. 39. Tiara superba, nov. sp.

PLATE. 16.

36.

37.

38.



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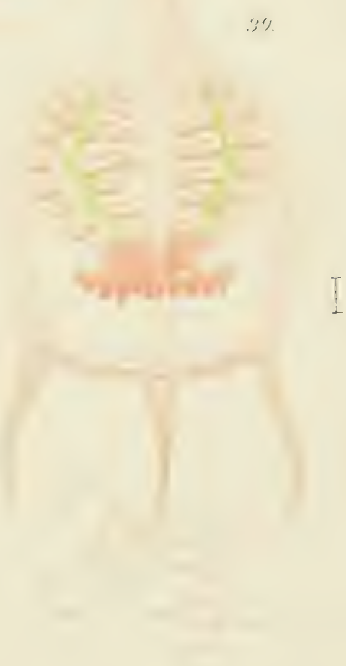


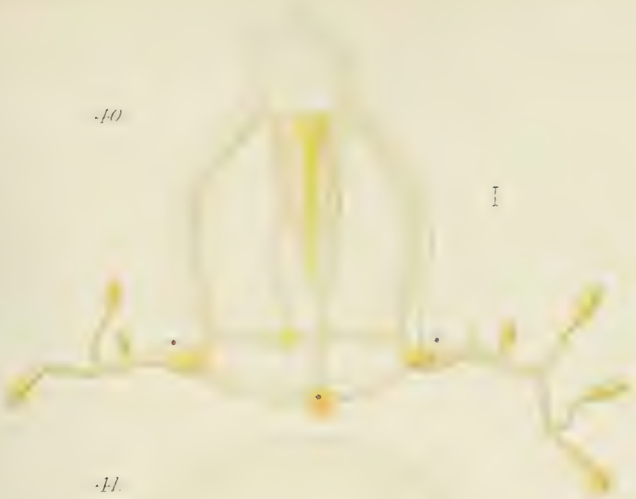
A.G.M.

B. Meisel lith. Boston

PLATE 17.

Fig. 40. Gemmaria dichotoma, nov. sp.
Fig. 41. Dipurena fragilis, nov. sp.

40.



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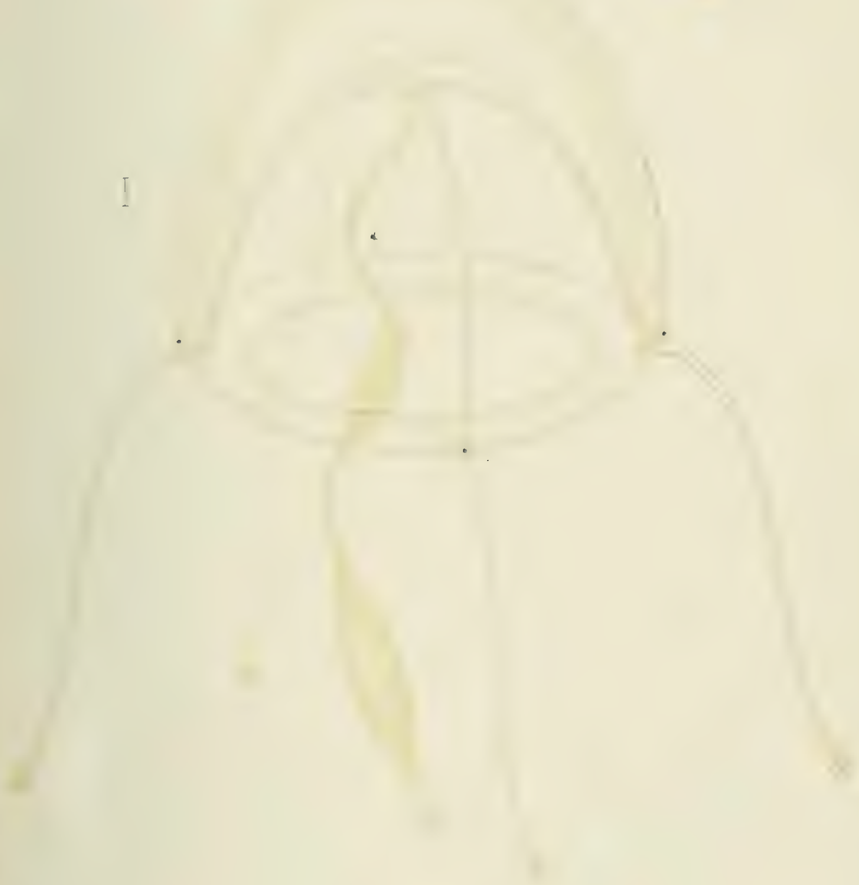

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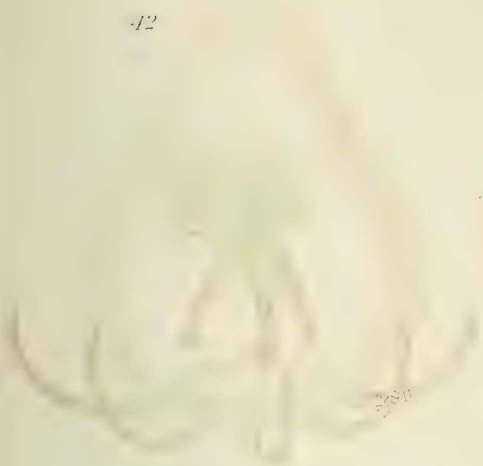
PLATE 18.

Fig. 42. Dysmorphosa minuta, nov. sp.
Fig. 43. Netocertoides brachiatum, nov. gen. et sp. Side view.
Fig. 44. " " Aboral view.
Fig. 45. Dipurena picta, nov. sp.
Fig. 46. " " Terminal portion of tentacle.
Fig. 47. Staurodiscus tetrastaurus, Haeckel. Young medusa.

42.



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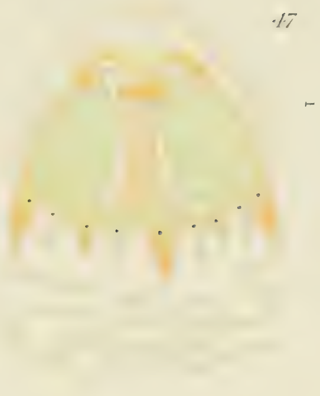

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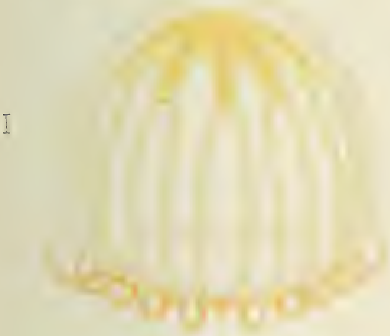

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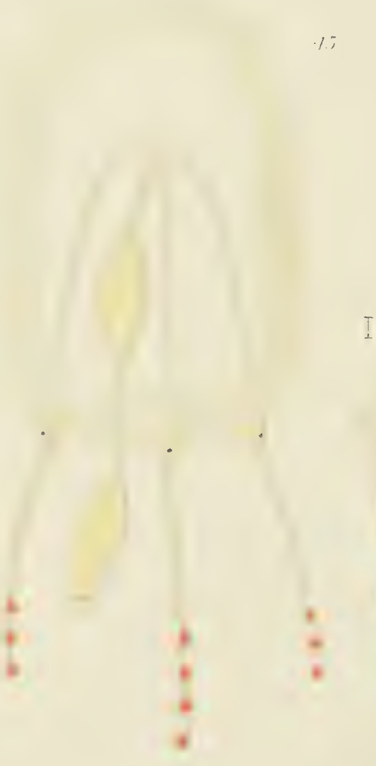

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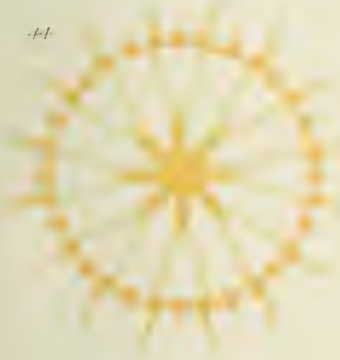

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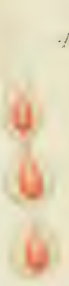
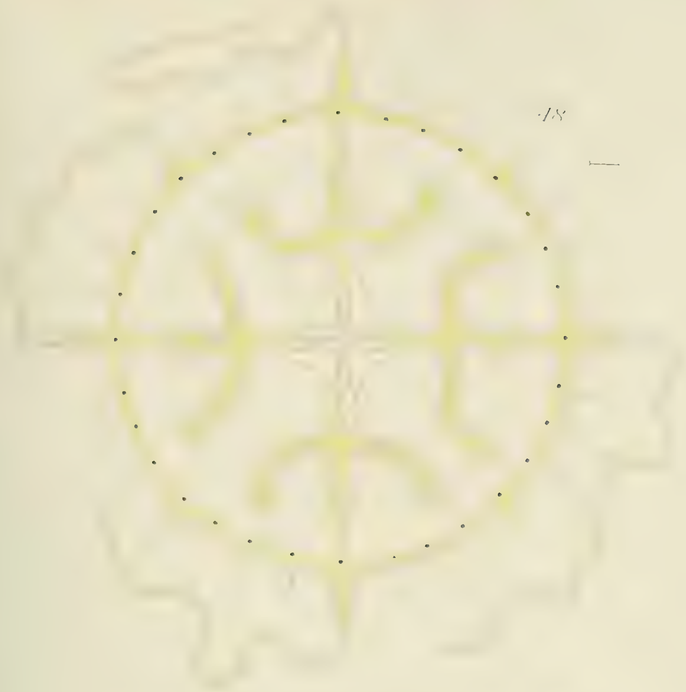


B. Meisel lith. Boston

PLATE 19.

Fig. 48. Staurodiscus tetrastaurus, Haeckel. Oral view of mature medusa.
Fig. 49. " " Side view of mature medusa.

18



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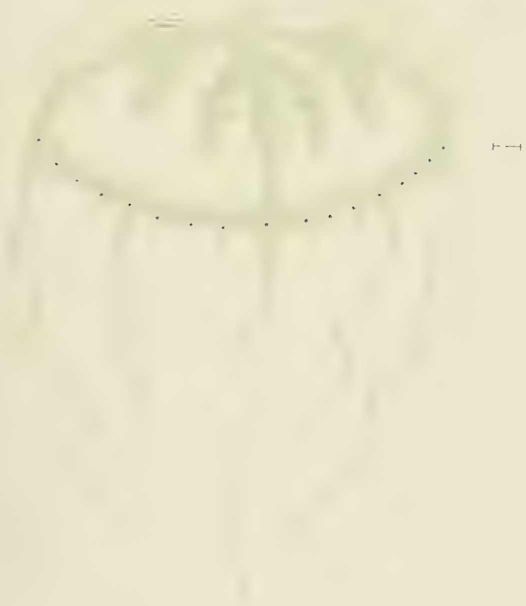
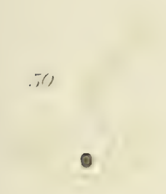


B. Meisel lith. Boston

PLATE 20.

Fig. 50. Laodicea neptuna, nov. sp. View of tentacle and ocellus.
Fig. 51. " " Side view of mature medusa.
Fig. 52. " " Oral view of mature medusa.
Fig. 53. Oceania discoida, nov. sp. Side view of mature medusa.
Fig. 54. " " Side view of young medusa.
Fig. 55. " " Oral view of bell margin of a young medusa.

50



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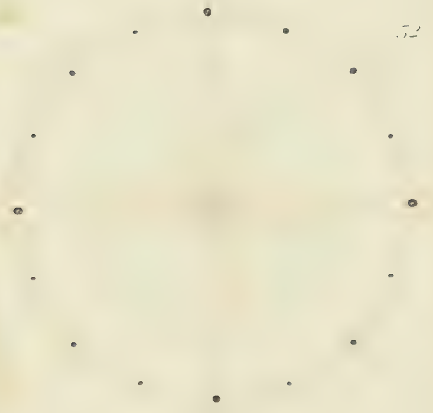

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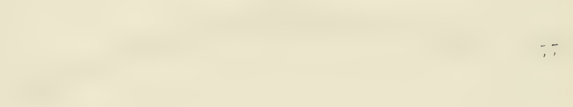


PLATE 21.

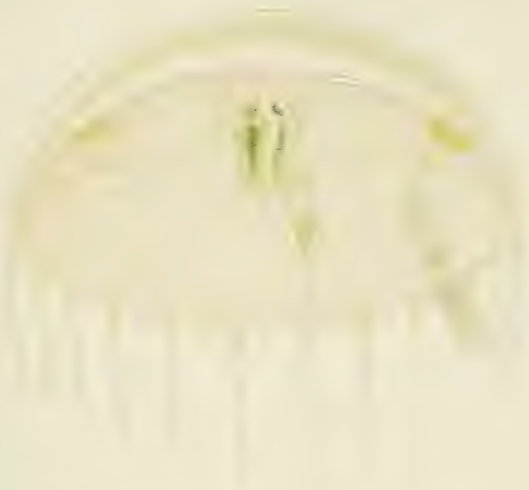
Fig. 56. Oceania McCradyi, Brooks. Side view of mature medusa.

Fig. 57. Oceania McCradyi, Brooks. View of one of the hydroid blastostyles that are produced upon the gonads.

Fig. 58. Oceania McCradyi, Brooks. Young blastostyle.

Fig. 59. " " " Oral view of mature medusa.

56



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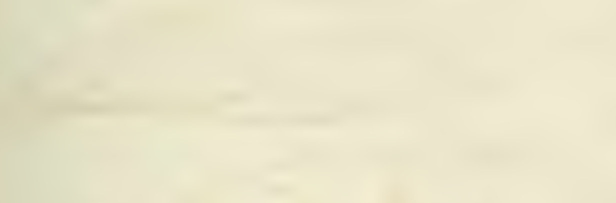

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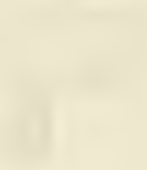

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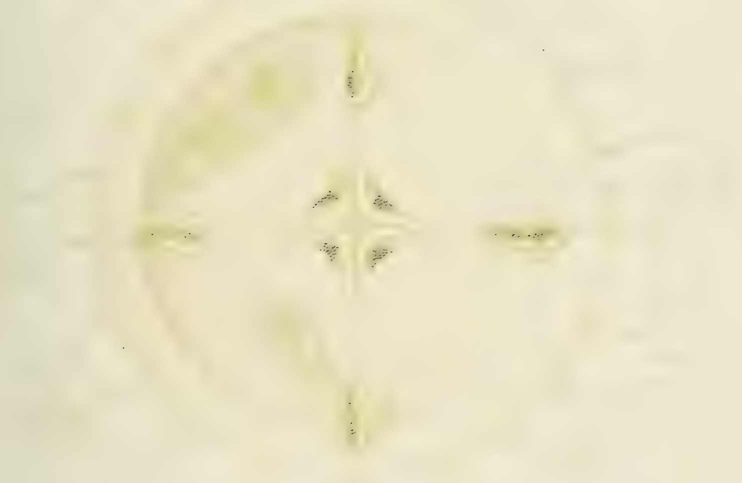
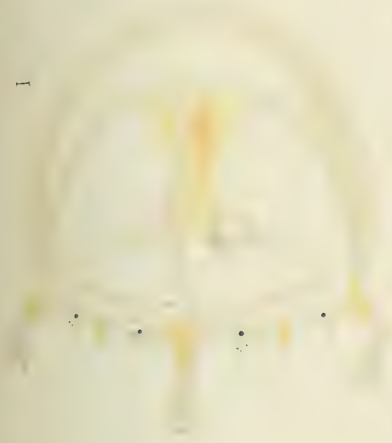


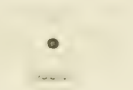
B. Meisel lith. Anst.

PLATE 22.

Fig. 60. Tiaropsis punctata, nov. sp. Young medusa.
Fig. 61. " " Medusa older than Fig. 60.
Fig. 62. " " Otocyst of young medusa.
Fig. 63. " " Otocyst of medusa drawn in Fig. 61.
Fig. 64. Dysmorphosa dubia, nov. sp. Side view.
Fig. 65. " " Oral region of the proboscis.
Fig. 66. " " Tentacle and ocellus.

60.





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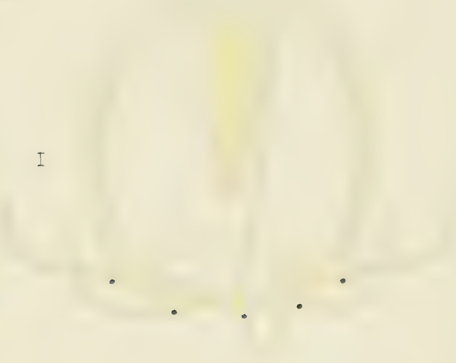

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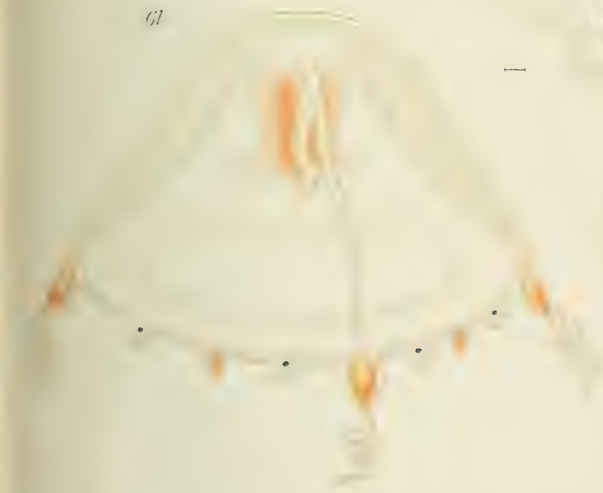
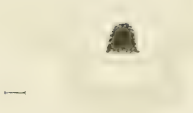


63.



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B Meisel lith Boston

PLATE 23.

Fig. 67. Nausithoë punctata, Kölliker. Oral view of young ephyra.
Fig. 68. " " Oral view of sense-organ of young ephyra.
Fig. 69. Eutimium serpentinum, nov. sp. Mature medusa.
Fig. 70. " " View of bell margin, and tentacle.
Fig. 71. " " Gastric portion of the proboscis.
Fig. 72. " " Proximal portion of the peduncle.

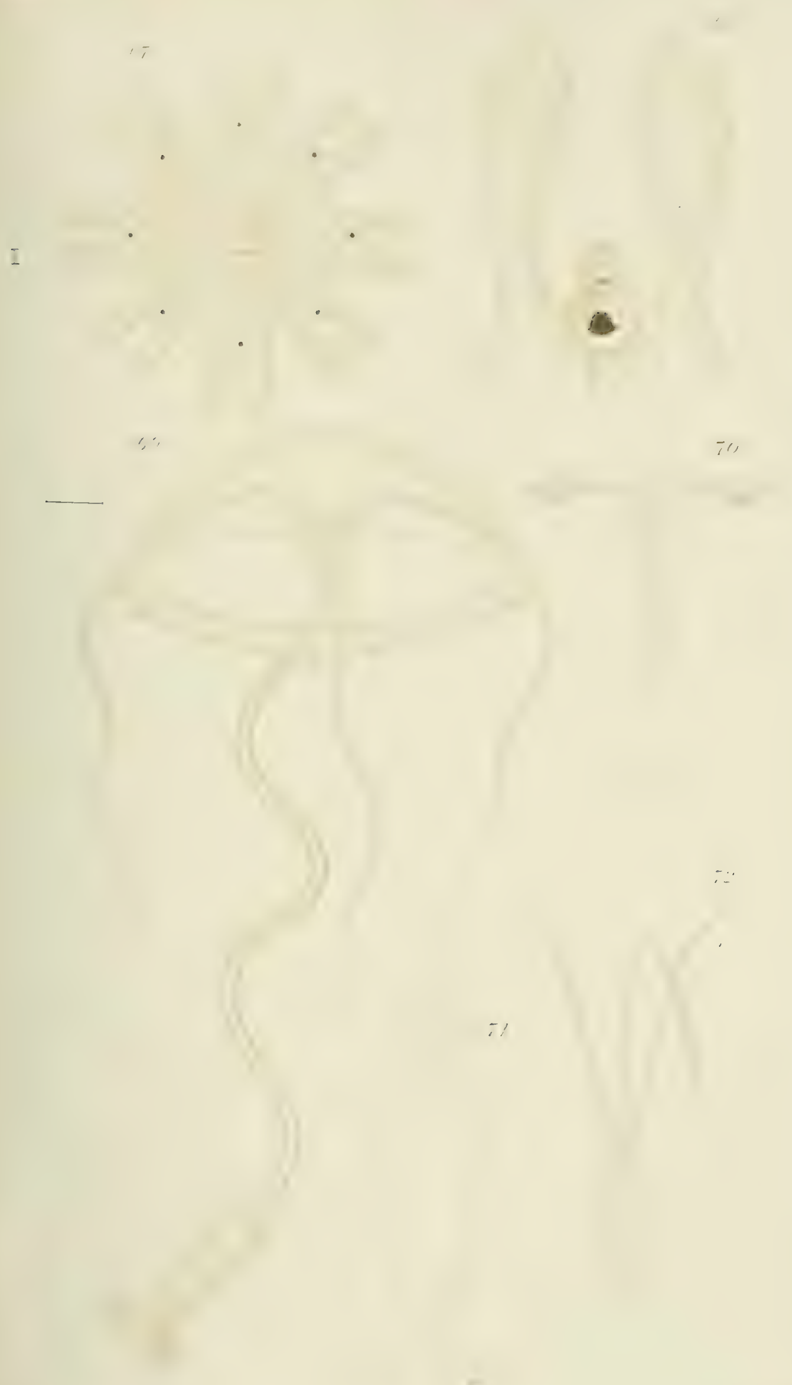
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PLATE 24.

Fig. 73.	Aurelia habanensis, nov. sp. View of the edge of the mouth-arms, or palps, showing the wart-like clusters of nematocyst cells.		
Fig. 74.	Aurelia habanensis, nov. sp. One of the wart-like clusters of nematocyst cells from the edge of the palps.		
Fig. 75.	Glossocodon tenuirostris, Fewkes. Mature medusa		
Fig. 76.	"	"	View of mouth.
Fig. 77.	"	"	View of ovary.
Fig. 78.	"	"	View of tentacle and otocyst.

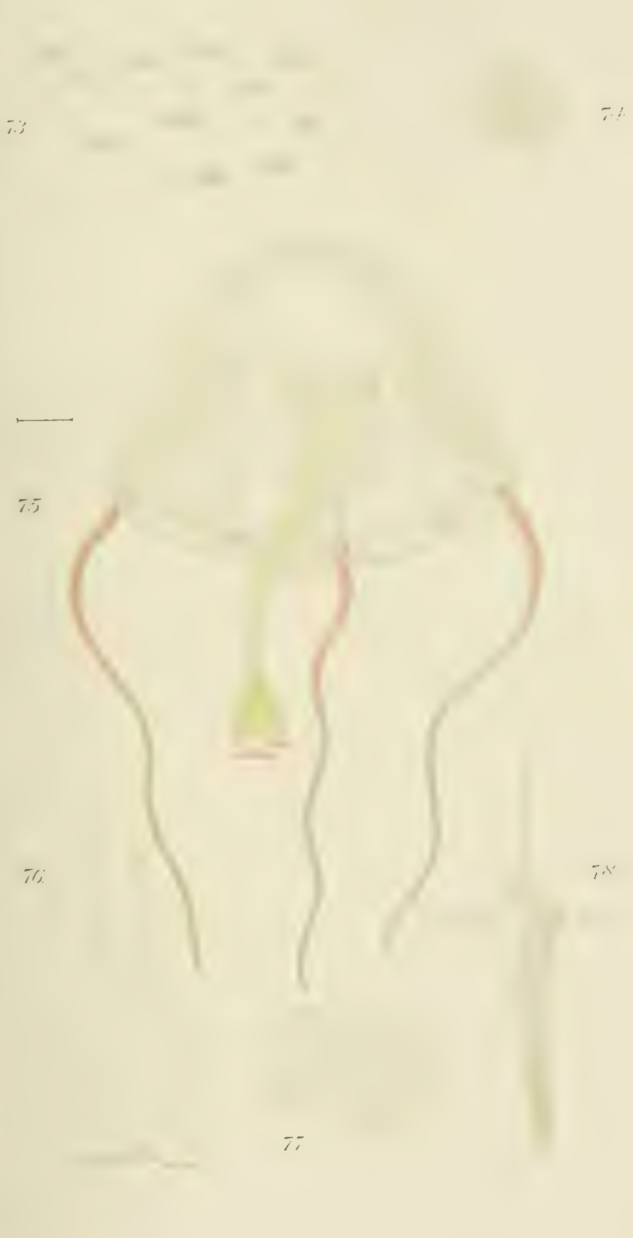
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PLATE 25.

Fig. 79. Aglaura hemistoma, Péron and Lesueur. Mature medusa.
Fig. 80. " " Otocyst.
Fig. 81. Charybdea aurifera, nov. sp. (*f*), frenula ; (*ms*) muscle strands ?
Fig. 82. " " Side view of rhopalium.
Fig. 83. " " View of rhopalium from without the bell.
Fig. 84. Zygodactyla cubana, nov. sp.
Fig. 85. " " View of bell margin.

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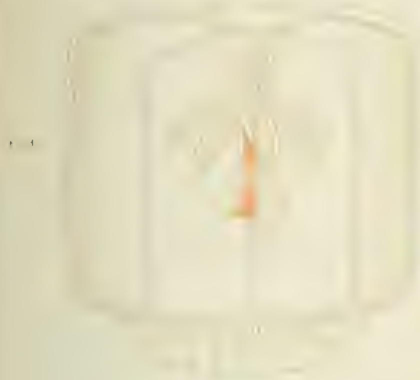

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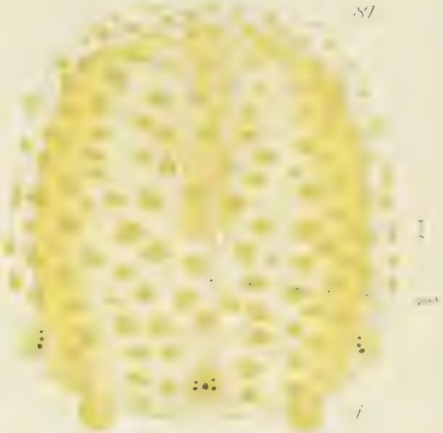

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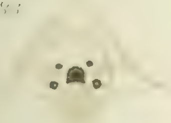

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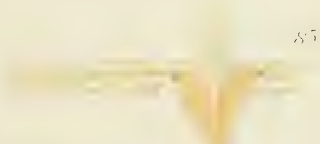

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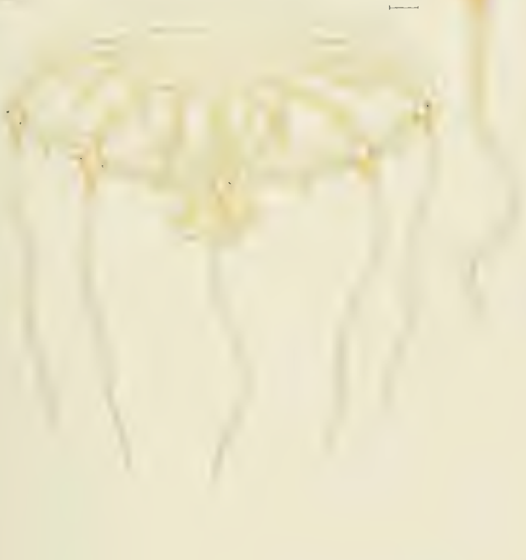
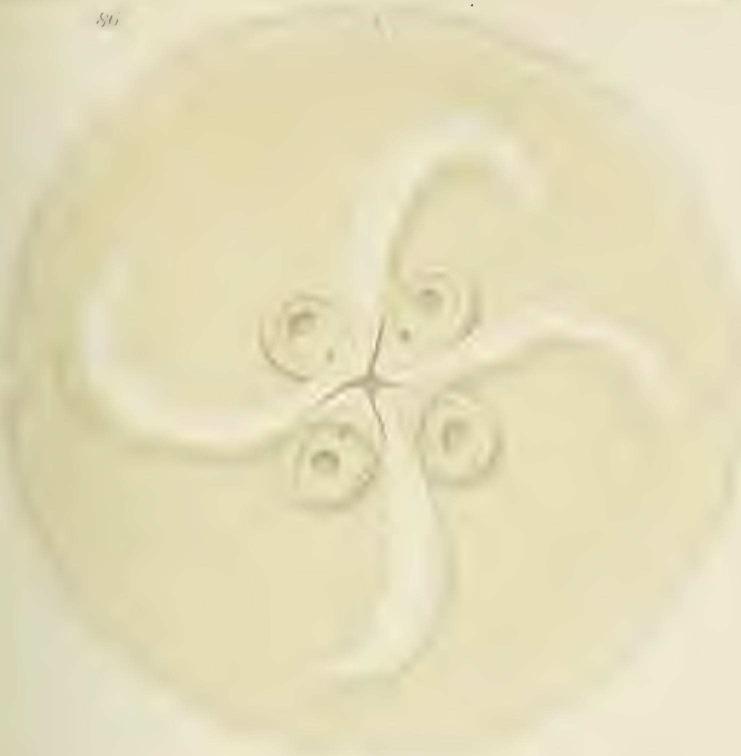


A.G.M. del.

PLATE 26.

Fig. 86.	Aurelia habanensis, nov. sp.	Oral view of mature medusa.
Fig. 87.	Nausithoë punctata, Kölliker.	Oral view of mature medusa.
Fig. 88.	" " "	Otocyst and ocellus.

86.



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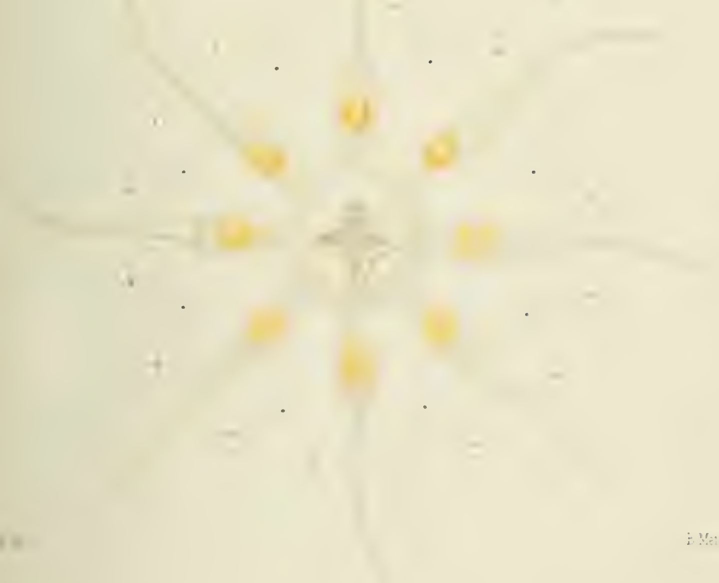

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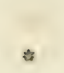

B. Meisel Lith Boston

PLATE 27.

Fig. 89. Sphæronectes gracilis, Haeckel. (*c*) connecting canal, (*f*) phyllocyst, (*p*) feeding-polypite, (*t*) tentacle.

Fig. 90. Chunia capillaria, nov. gen. et sp.

Fig. 91. Bolina vitrea, L. Agassiz. Mature animal.

Fig. 92. Bolina vitrea, L. Agassiz. View of apical sense-organ. (*c*) gastric cilia ; (*f*) funnel ; (*mu*) "muscle" fibres.

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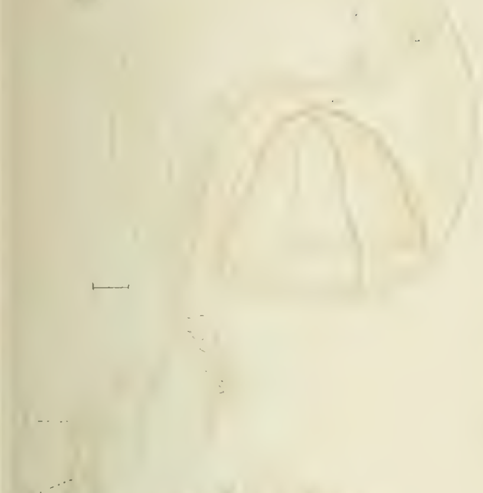

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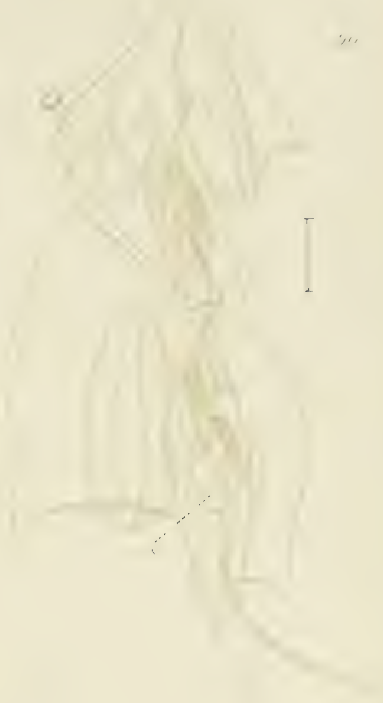

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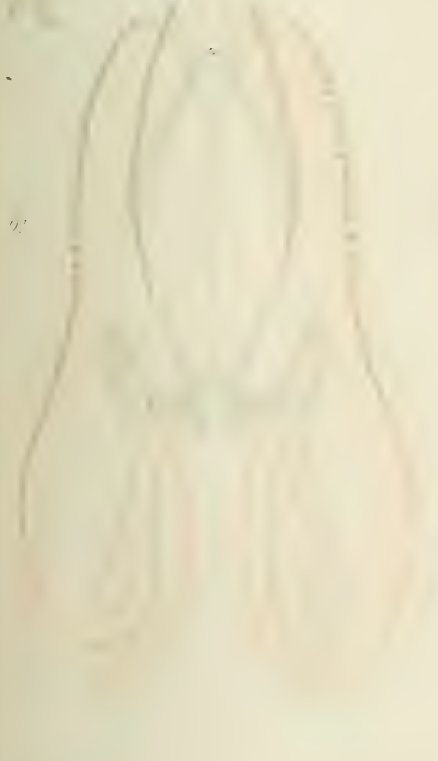

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PLATE 28.

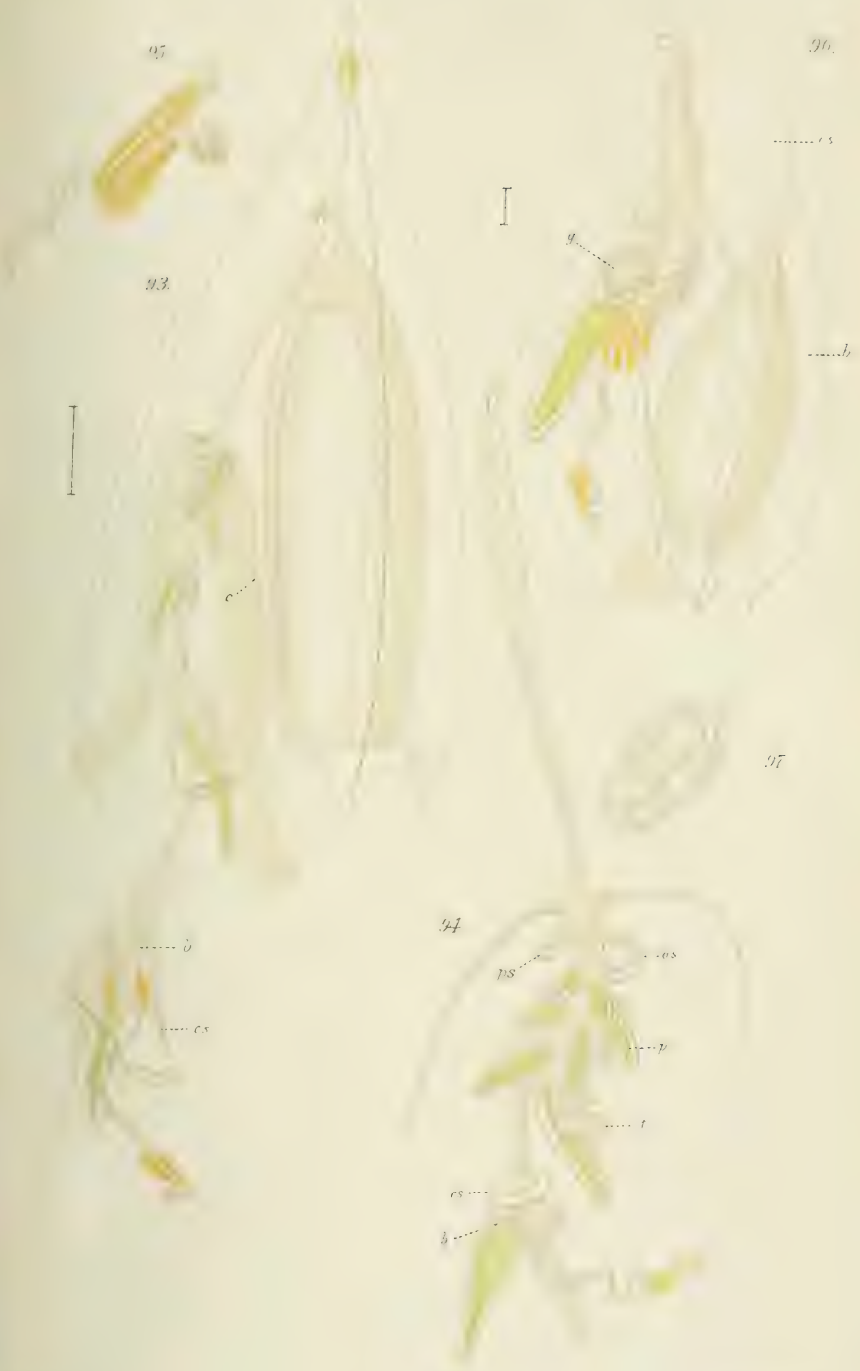
Fig. 93. Diphyopsis campanulifera, Chun. Side view of mature animal. The posterior swimming-bell has been lost through accident.

Fig. 94. Diphyopsis campanulifera. Enlarged view of the proximal portion of the siphosome. (*ps*) place of origin of the large posterior swimming-bell that has been lost through accident; (*as*) small "reserve" swimming-bell; (*p*) feeding-polypite; (*t*) tentacle; (*cs*) covering scale, or bract; (*b*) immature swimming-bell (shown mature in Fig. 96, *b*).

Fig. 95. Diphyopsis campanulifera. Tentacular nematocyst battery.

Fig. 96. Ersæa Lessonii, Chun. The monogastric, sexual generation of **D.** campanulifera. (*b*) swimming-bell; (*cs*) apical bract, or covering scale; (*g*) gonophore.

Fig. 97. Ersæa Lessonii. Young ♀ gonophore containing two ova.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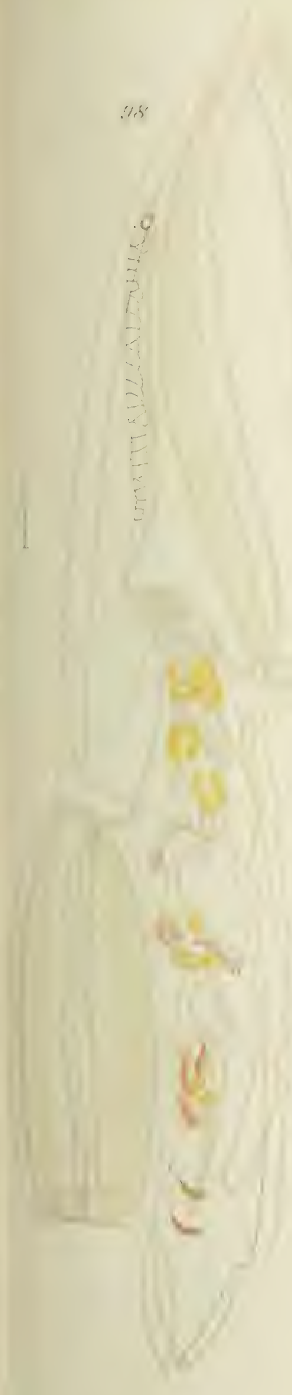
A.G.M. del.

E. Meisel lith. Boston

PLATE 29.

Fig. 98. Diphyopsis hispaniana, nov. sp.
Fig. 99. " " Portion of the siphosome.
Fig. 100. Ersæa hispaniana, nov. sp. The monogastric, sexual generation of Diphyopsis hispaniana. (*g*) gonophore.

98



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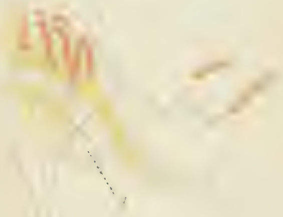

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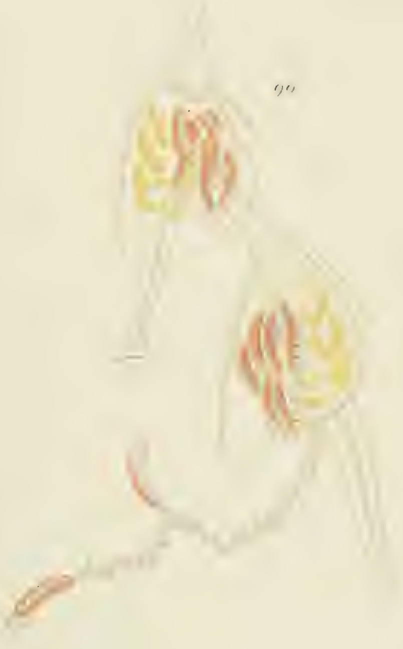


PLATE 30.

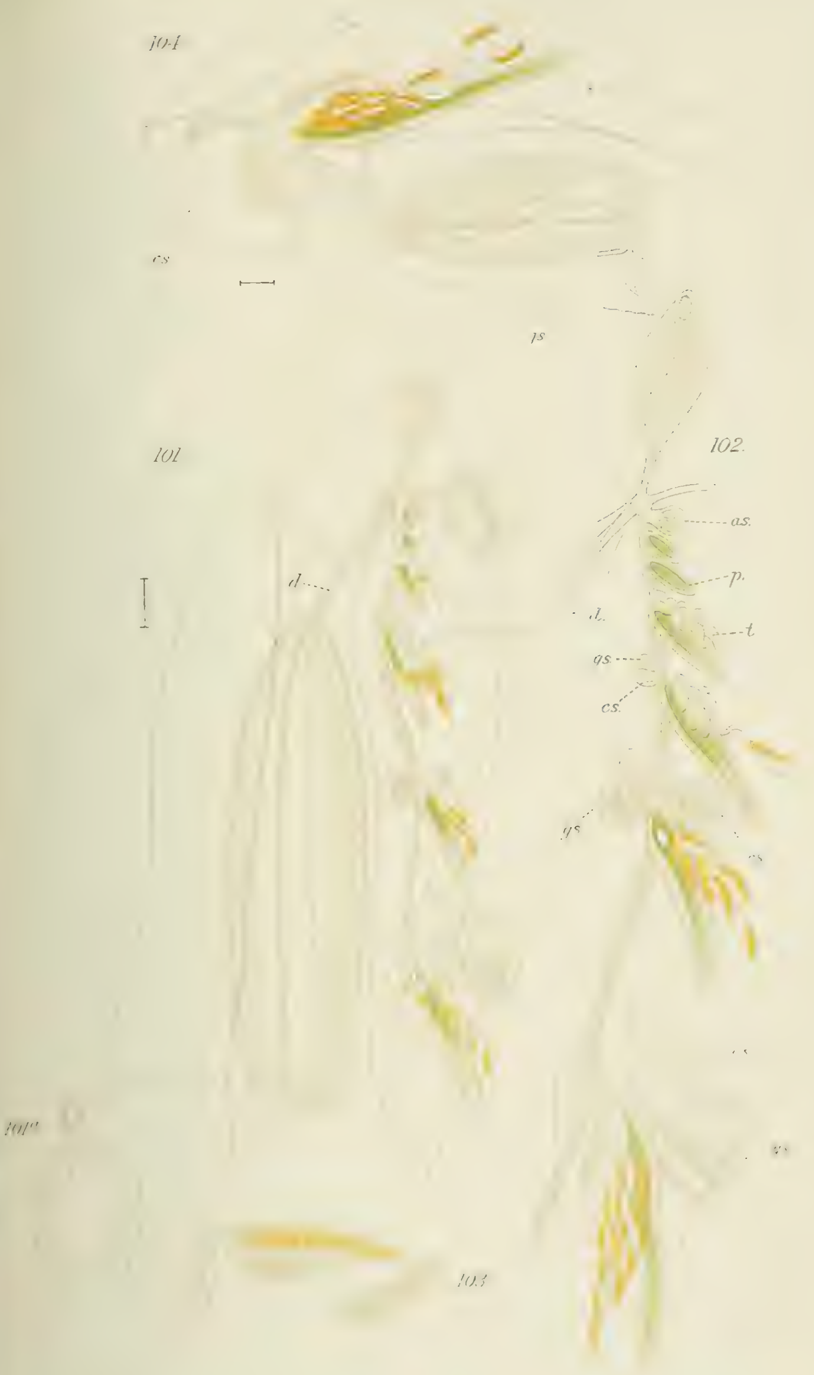
Fig. 101. Abyla pentagona, Eschscholtz.

Fig. 101^a. “ “ Usual form of the phyllocyst.

Fig. 102. “ “ Enlarged view of the siphosome. (*as*) small “reserve” swimming-bell; (*cs*) bract, or covering scale; (*d*) duct of the large posterior swimming-bell; (*gs*) medusiform gonophore.

Fig. 103. Abyla pentagona. Tentacular nematocyst battery.

Fig. 104. Aglaisma cuboides, Chun. The monogastric, sexual generation of Abyla pentagona. (*cs*) bract, or covering scale; (*gs*) medusiform gonophore that functions also as a swimming-bell.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B. Meisel lith Boston

PLATE 31.

Fig. 105. Ocyroë crystallina, Rang. Figure 1¼ times the natural size. (*w*) wart-like protuberances upon the surface of the Ctenophore; (*au*) auricle.
Fig. 106. Agalma Pourtalesii, Agassiz and Mayer. Female gonads.
Fig. 107. " " Male gonad.

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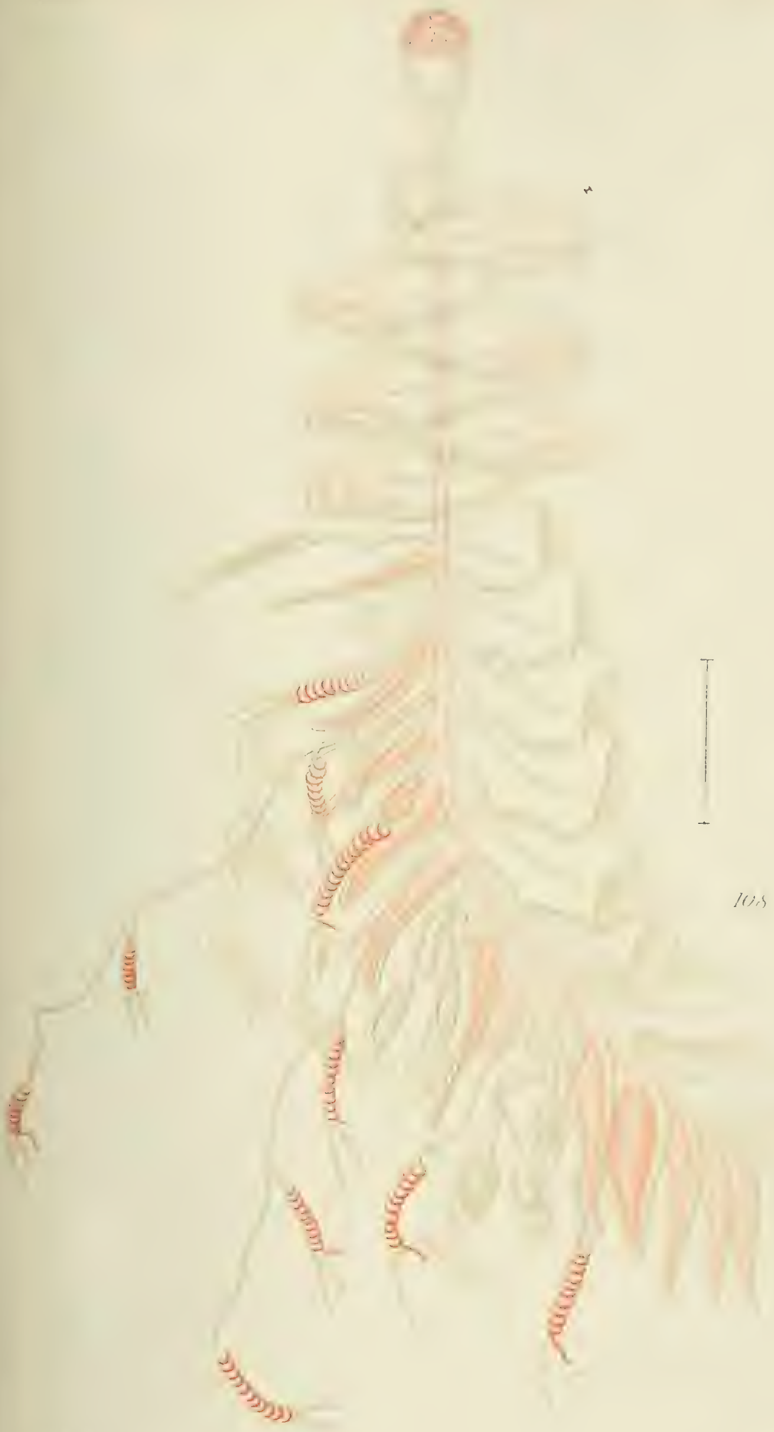
B. Meisel lith Boston

PLATE 32.

Fig. 108. Agalma Pourtalesii, Agassiz and Mayer. Side view of the entire animal. From a specimen obtained at the Tortugas, Florida.



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A.G.M. del.

B Meisel lith. Boston.

PLATE 33.

Fig. 109. Agalma Pourtalesii, Agassiz and Mayer. Swimming-bell seen from above.
Fig. 110. Agalma Pourtalesii. Swimming-bell seen from the side.
Fig. 111. “ “ Terminal portion of tentacle.
Fig. 112. “ “ View of a detached bract.
Fig. 113. “ “ Nematocyst-bearing papillæ sometimes seen on young and immature bracts.

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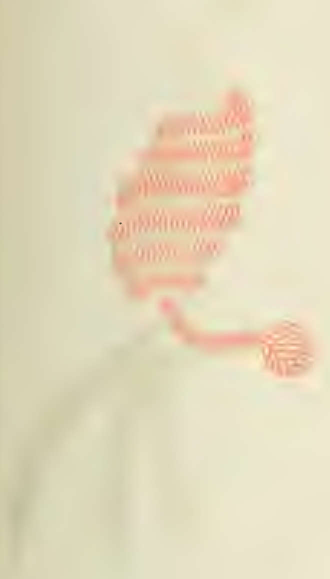

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B Meisel lith Boston

PLATE **34**.

Fig. 114. Diphyes bipartita, Costa.

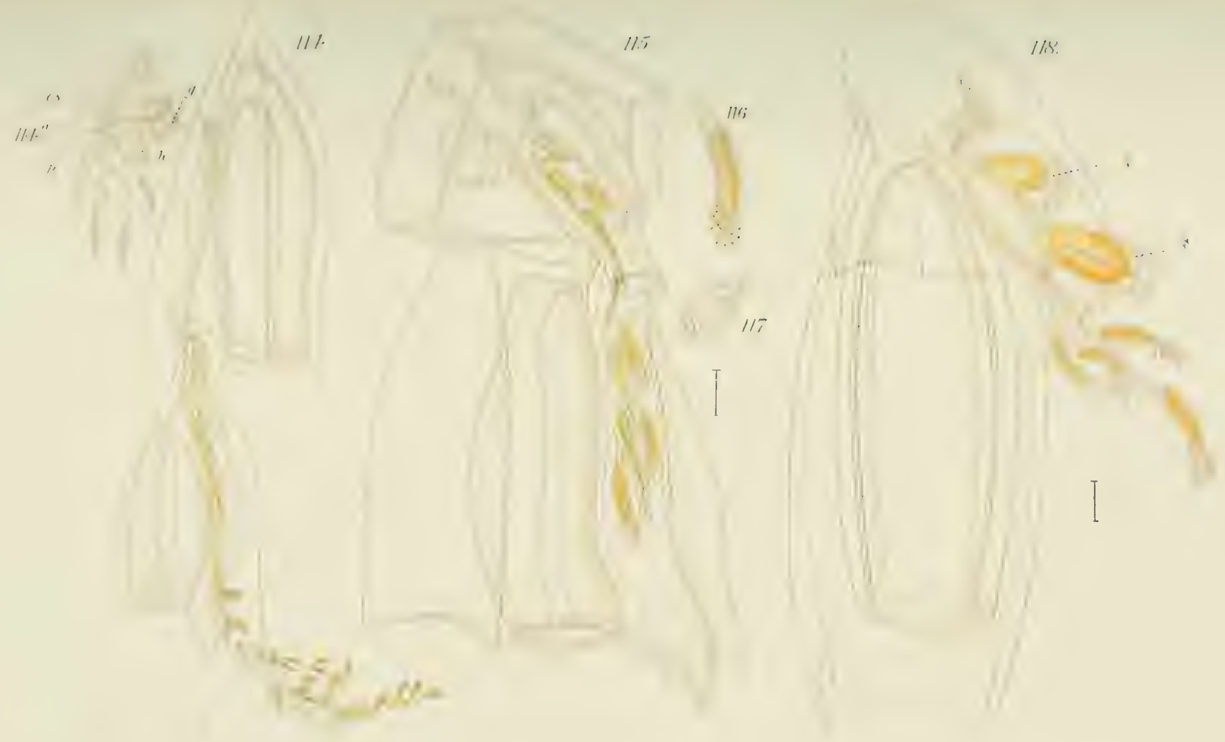
Fig. 114^{a}. “ “ One of the units of the siphosome. (*g*) medusiform gonad, (*h*) siphosome, (*p*) feeding-polypite, (*t*) tentacle, (*cs*) covering scale or bract.

Fig. 115. Abyla quincunx = Abylopsis quincunx, Chun.

Fig. 116. “ “ Tentacular nematocyst battery.

Fig. 117. “ “ Small “ reserve ” swimming-bell.

Fig. 118. Ersæa picta, Chun.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A.G.M. del

B. Meisel lith Boston

PLATE 35.

Fig. 119. Agalma virida, nov. sp. Immature individual.
Fig. 120. " " Terminal knob of the tentacles.
Fig. 121. " " Polygonal pigment cells of the float.

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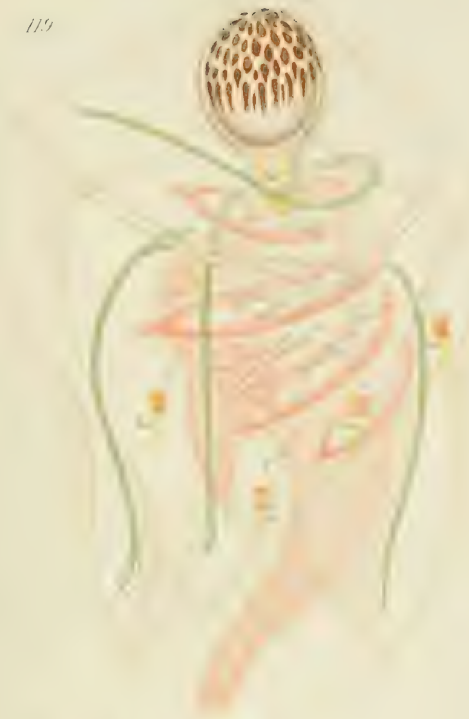

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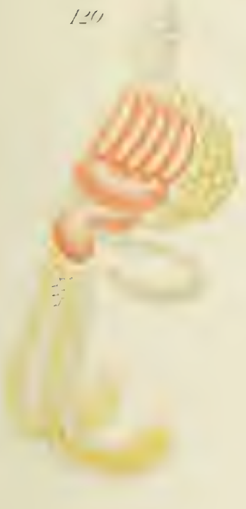

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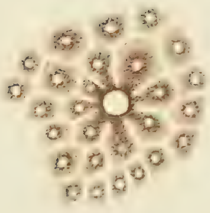

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B. Meisel lith Boston

PLATE 36.

Fig. 122. Cytaeis gracilis, nov. sp. Mature medusa.
Fig. 123. " " Young medusa.
Fig. 124. " " Very young medusa.

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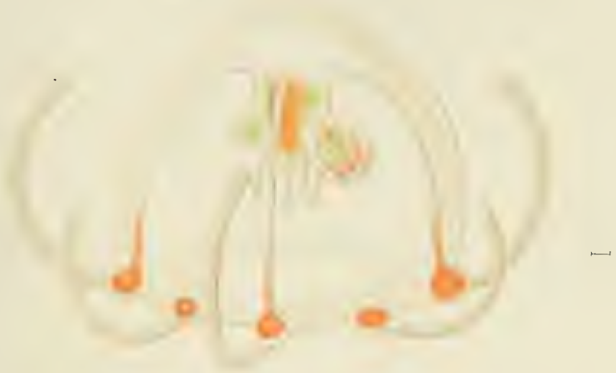

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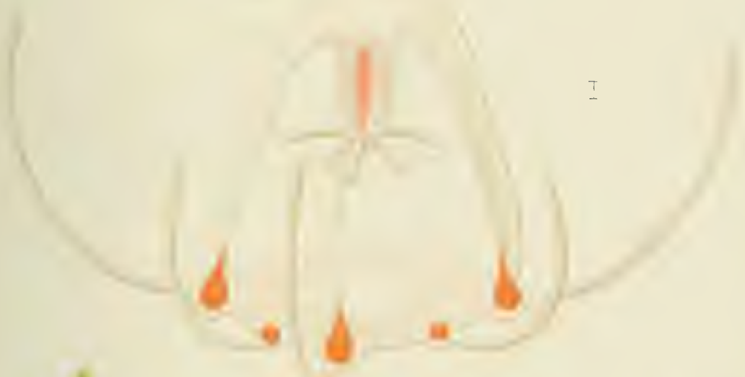

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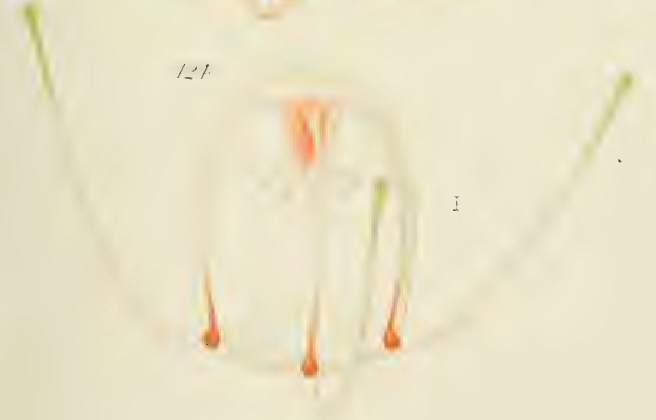

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PLATE 37.

Fig. 125. Ectopleura minerva, nov. sp.
Fig. 126. Dinema jeffersoni, nov. sp.

PLATE 37.

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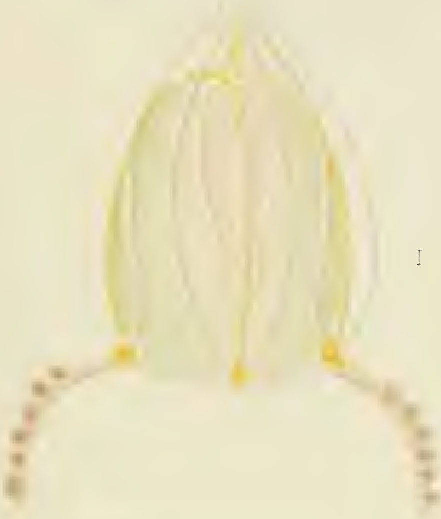

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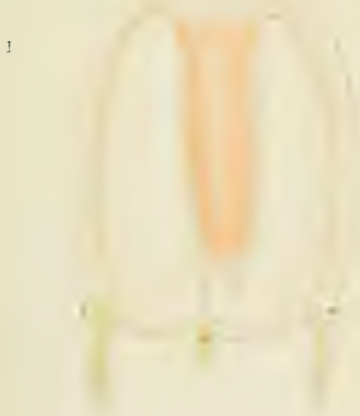

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PLATE 38.

Fig. 127. Lizzia elegans, nov. sp.
Fig. 128. Eucheilota ventricularis, McCrady.

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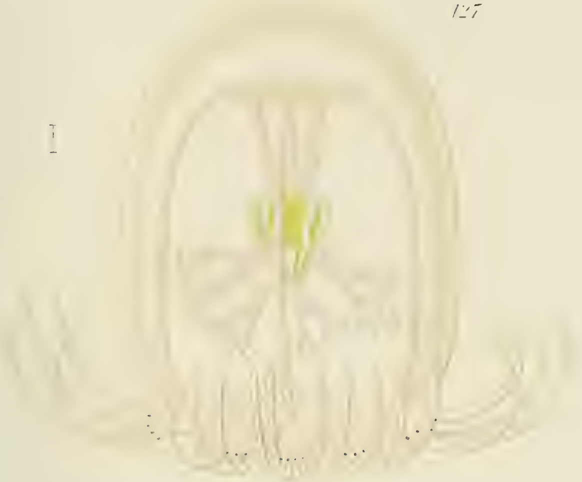

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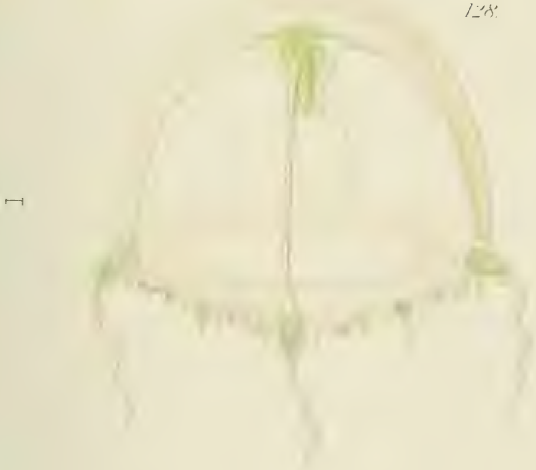

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B. Meisel lith. Boston

PLATE 39.

Figs. 129, 130. Multioralis ovalis, nov. gen. et sp.
Fig. 131. Pseudoclytia pentata, nov. gen. et sp. Side view of mature medusa ♀.
Fig. 132. " " Tentacle-bulb showing green entodermal pigment.

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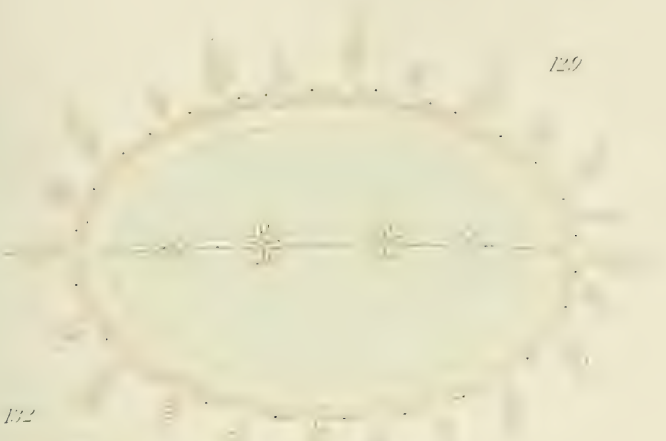

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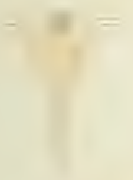

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PLATE 40.

Fig. 133. Phortis lactea, nov. sp.
Fig. 134. Eucheilota paradoxica, nov. sp.
Fig. 135. " " A young medusa bud.
Fig. 136. " " A medusa bud about to be set free from the parent.

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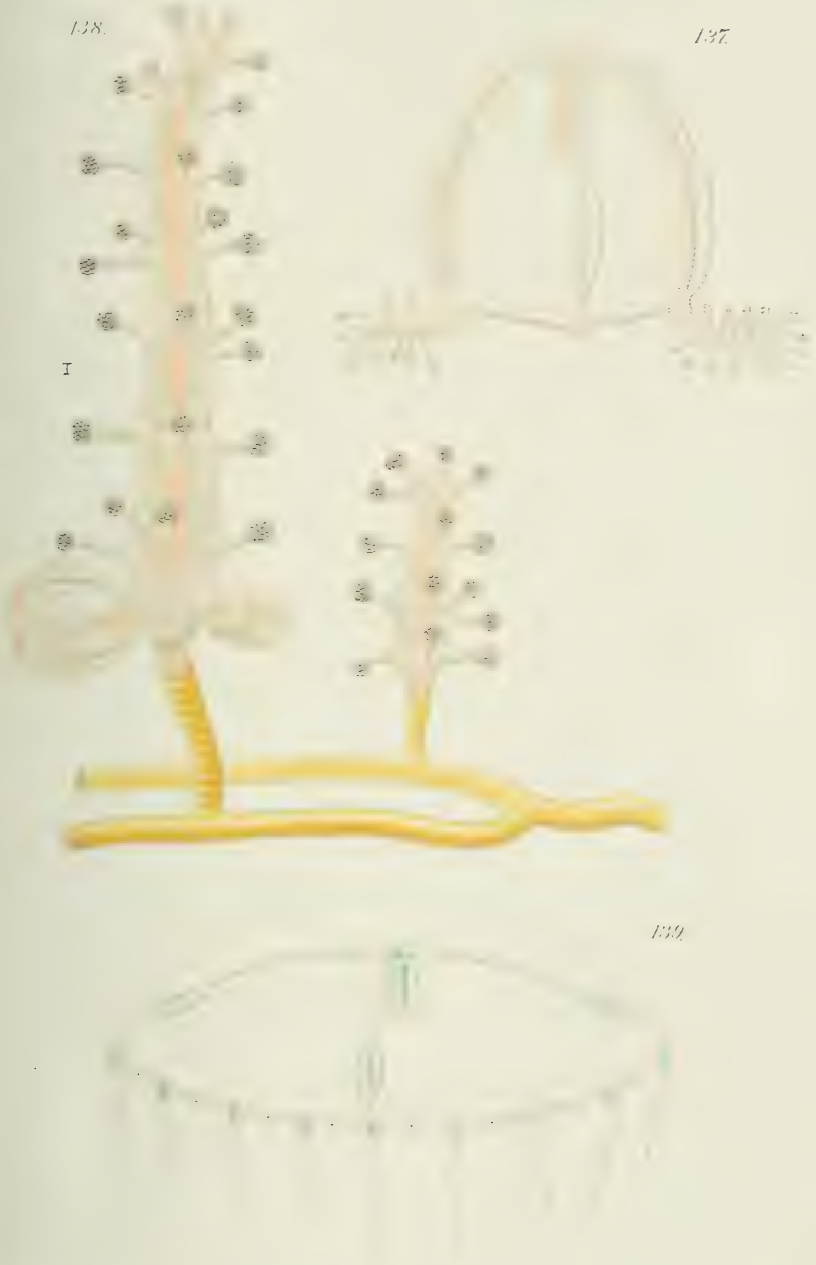
[illegible]

B. Meisel lith. Boston.

PLATE 41.

Fig. 137. Zanclea gemmosa, McCrady. Young medusa of Gemmaria gemmosa.
Fig. 138. Gemmaria gemmosa, the hydroid stock of Zanclea gemmosa, McCrady.
Fig. 139. Epenthesis folleata, McCrady. Adult medusa.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B. Meisel lith. Boston.

PLATE 42.

Fig. 140. Eucopium parvigastrum, nov. sp. Adult medusa.

Fig. 141. Niobia dendrotentacula, nov. gen. et sp. Side view of an adult medusa.

Fig. 142. Niobia dendrotentacula. A young medusa recently separated from the adult individual.

Fig. 143. Niobia dendrotentacula. The proboscis and ova of a mature medusa after the cessation of the medusa-forming process.

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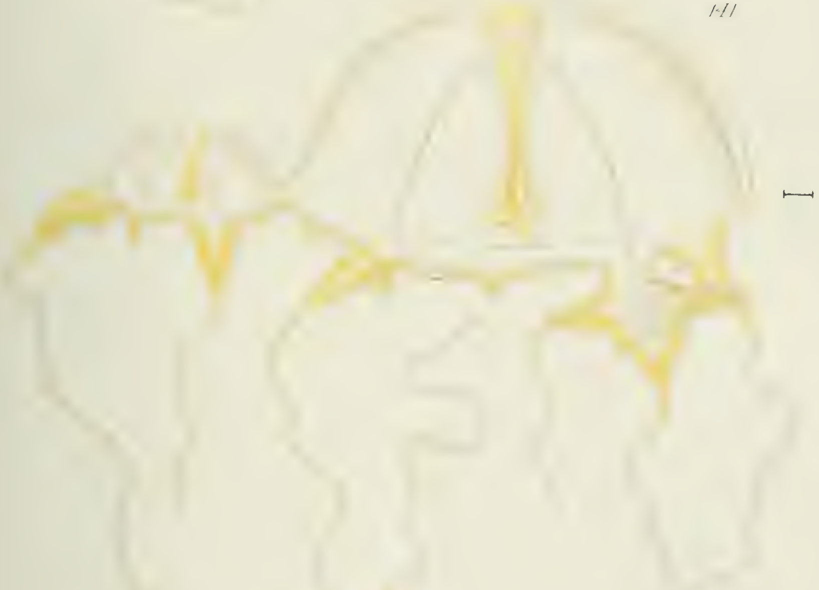

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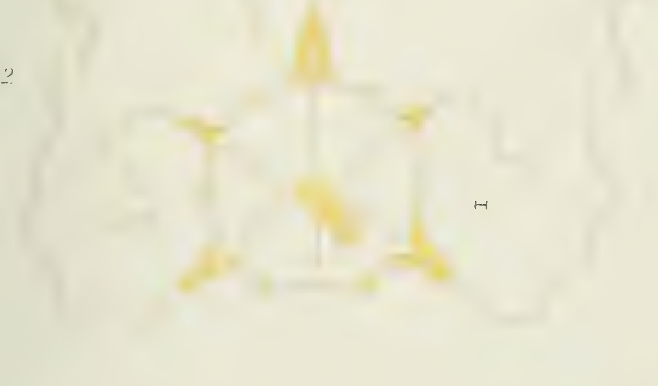

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PLATE 43.

Fig. 144. Niobia dendrotentacula, nov. gen. et sp. Oral view of an adult medusa, showing stages in the formation of new medusæ from the tentacle bulbs of the parent form.

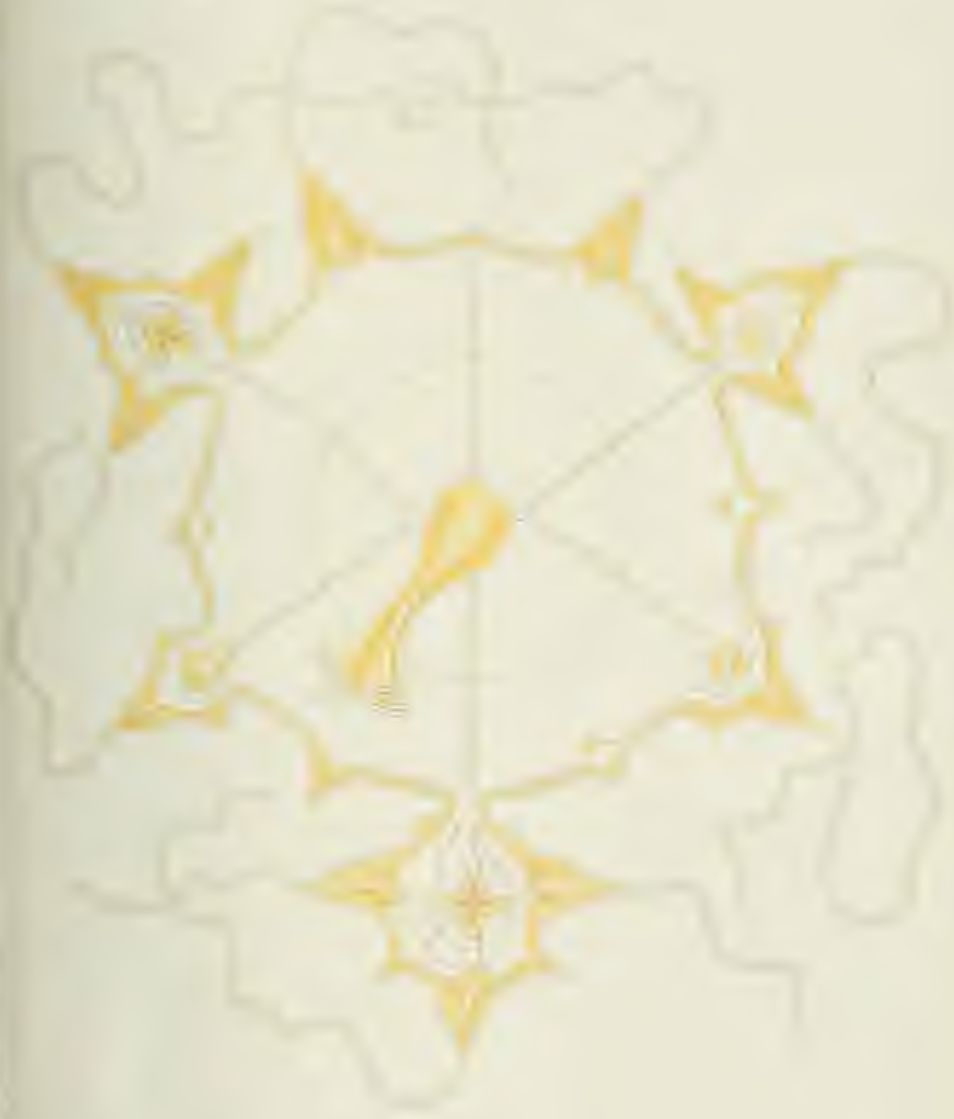

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PLATE **44**.

Fig. 145. Cunoctantha incisa, nov. sp. Oral view.
Fig. 146. " " " Side view.

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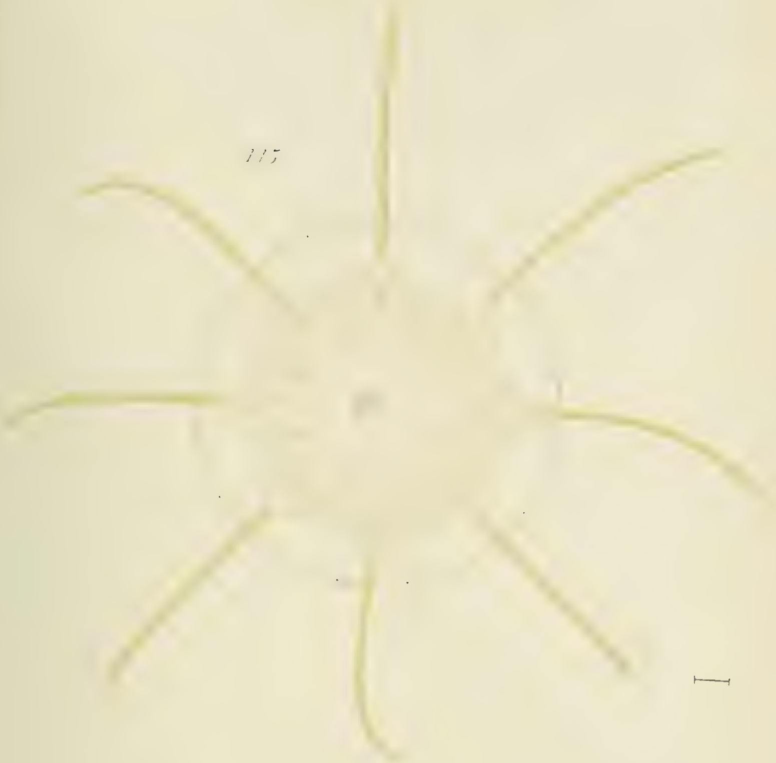

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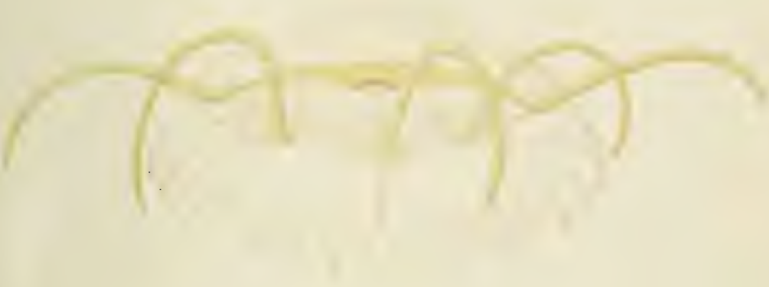

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Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
VOL. XXXVII. No. 3.

THE REGENERATING NERVOUS SYSTEM OF LUMBRICIDÆ AND THE CENTROSOME OF ITS NERVE CELLS.

BY HERBERT W. RAND.

WITH EIGHT PLATES.

CAMBRIDGE, MASS., U. S. A.:
PRINTED FOR THE MUSEUM.
SEPTEMBER, 1901.

I. Introduction.

For several years after the description by van Beneden, in 1883, of the mitotic polar structures to which he gave the names, "sphères attractives" and "corpuscules polaires," such structures were observed only in cells undergoing mitosis, and were believed to be visibly present only during the mitotic process, although it was suggested by van Beneden himself that they might be preformed in the cell, becoming evident only during mitosis. It was therefore a matter of some interest when, in 1891, Flemming described structures in certain resting cells of the salamander similar to those found at the poles of the mitotic figure. Flemming was the first to describe these structures minutely, although the observations of Solger ('89) and Rabl ('89) had been made previously.

This discovery led to the search for the centrosome in the resting cells of various tissues, and interest in the question culminated with the announcement by von Lenhossék, in 1895, of the discovery of a centrosome and sphere in the nerve cells of the frog. Von Lenhossék was quickly followed by other authors who described similar structures in the nerve cells of other animals, and at the present time the "centrosome" is known to exist in the nerve cells of many vertebrates and invertebrates.

It is a matter of some importance, as has been pointed out by several authors, to determine whether or not the "centrosomes," "spheres," and radiations seen in the cytoplasm of fully differentiated and presumably functional nerve cells are related to the polar structures of past or future mitotic divisions of the cell. Accepting the general belief that functional nerve cells do not divide, we are limited to proving either that the centrosome and its accompanying structures of the last mitosis of the embryonic nerve cell persist as the centrosome and radiating system of the differentiated nerve cell, or that, on the contrary, they do not persist, and that we have to do in the differentiated nerve cell with structures which have arisen in the cytoplasm independently of the last mitosis of the cell. That certain parts of the radiating system of the resting cell could have been left over from the last division, and other parts not, is, of course, a possibility to be considered.

The following work was undertaken at the suggestion of Professor E. L. Mark, with the purpose of throwing some light upon the origin of the so-called centrosome of the nerve cell. The work was carried on at Harvard University under the direction of Professor Mark and Doctor W. E. Castle, from whom have been received much valuable assistance and many helpful suggestions as to the proper interpretation of the results obtained.

II. Historical.

1. The Centrosome in Nerve Cells.

Previous to von Lenhossék's discovery, in 1895, of the centrosome in the nerve cell, we find in the literature a few references to a fibrillar structure of the cytoplasm of nerve cells and a concentric arrangement about the nucleus.

Remak (**'44**, p. 469) described in the nerve cells of Astacus "sehr zarte granulirte, den Kern umkreisende Fasern." In the nerve cells of Raja he (**'53**) mentions two systems of fibrillæ, — peripheral ones extending into the axis cylinder, and deeper ones concentric to the nucleus.

Walter (**'63**), Leydig (**'64**, p. 84), Arnold (**'67**), and Schwalbe (**'68**) found a fibrillar structure concentric to the nucleus in nerve cells of vertebrates and invertebrates.

Arnold (**'65, '67**), Courvoisier (**'66**), Sigmund Mayer (**'72**), Eimer (**'77**), and other authors speak of fine fibres extending out from the nucleus, or even from the nucleolus, in vertebrate nerve cells, but from the descriptions and figures given it is impossible that these structures could have been identical with the exceedingly delicate radiations recently observed in connection with the centrosome.

Max Schultze (**'71**) found fibrillæ concentric to the nucleus in certain brain cells of Torpedo, as well as fibrillæ which enter the cell from the processes.

Hans Schultze (**'79**) described fibrillæ concentric to the nucleus in nerve cells of vertebrates.

Flemming (**'82, '82^a**) mentioned a "streifige Structur" concentric to the nucleus in the central nerve cells of the pig. In the cells of the spinal ganglion of various mammals he found a fibrillar structure, but it exhibited no concentric or radial arrangement.

Von Lenhossék (**'86**) figured and described, in the spinal-ganglion cells of the frog, an arrangement of fibrillæ generally, but not always, concentric to the nucleus. In some of his figures the nuclei are very excentrically placed and are flattened or even slightly concave on the side nearest the centre of the cell, agreeing in this respect with the conditions found in his later work on the same material, in which the centrosome and sphere were discovered.

Heidenhain (**'94**) declared that the presence of a centrosome was least to be expected in nerve cells. Nevertheless, he pointed out that the evidences of radial and concentric arrangement which have been described in such cells demand that a careful search for the centrosome be made.

Flemming (**'95**) mentioned the frequent occurrence of the concentric arrangement in the nerve cells of many animals investigated by him. He says (p. 25): "Die Anordnung ist nicht im vollen Sinne concentrisch, sondern scheint von der Polstelle in zwei opponirten Strahlungen an der Peripherie der Zelle zu verlaufen, so dass der Kern etwa die Mitte zwischen beiden bildet."

Von Lenhossék (**'95**), after the demonstration by Flemming and Heidenhain of the centrosome in resting cells, returned to the study of the nerve cells in which the excentric and flattened nuclei had been observed, and by methods other than those used in his previous work demonstrated the presence of a centrosome and sphere. The conditions which he finds in some of the spinal-ganglion cells of the frog are briefly as follows.

The nucleus is in a very excentric position and generally flattened, or even concave, on the side nearest the cell centre. The centrosome and sphere lie at the centre of the cytoplasmic mass, *exclusive of the nucleus;* for, as a result of planimetric measurements, von Lenhossék declares that "das Centrosom ist also in den Spinalganglien des Frosches wohl ein Centralgebilde in Bezug auf das Zellprotoplasma mit Abzug des Kerns, nicht aber in Bezug auf die kernhaltige Gesammtzelle" (p. 367). Heidenhain had found that in leucocytes the "Microcentrum" occupied the geometrical centre of the entire cell, except when displaced by a nucleus greater than one-half the diameter of the cell.

The centrosome of von Lenhossék is about 0.5 μ in diameter, and is composed of never fewer than twelve granules imbedded in a feebly staining matrix, which he compares to the "achromatische Substanzmasse" by which Heidenhain's "Centralkörper" were connected. Surrounding this group of granules is the sphere, which appears in sections as a sharply defined, homogeneous, circular area from 4 μ to 6 μ in diameter. Its sharp boundary is not due to a layer of microsomes, but is marked only by the contrast between the substance of the sphere and the surrounding cytoplasm. This contrast is often emphasized by a narrow clear area about the sphere.

The cytoplasm is arranged concentrically around the sphere, showing a differentiation into an endoplasm and an exoplasm. The endoplasm is finely granular, the granules being more concentrated toward the centre. The exoplasm gives up its stain more readily than the endoplasm, remaining diffusely stained and appearing less granular than the endoplasm.

The conditions described were found in only the smaller cells of the ganglia. No centrosome was found in the spinal-ganglion cells of the dog or cat, but a concentric arrangement of the cytoplasm about the nucleus, which in those animals was found generally at the cell centre, was observed, leading von Lenhossék to suggest (p. 368) that "das dynamische oder vielleicht auch morphologische Aequivalent des Centrosoms hier in den Kern verlagert ist." No radiations were seen by von Lenhossék. All of his figures are from preparations fixed in sublimate and stained by Heidenhain's bordeaux-iron-hæmatoxylin method.

Bühler ('95), working simultaneously with von Lenhossék, announced the discovery of "Centralkörper" in the cortex of the fore-brain of the lizard, and also in nerve cells of the human brain. Bühler used warm corrosive sublimate and Flemming's fluid as fixing agents, and stained in various aniline dyes. His best demonstration of the "Centralkörper," however, resulted from the use of Heidenhain's iron-hæmatoxylin with bordeaux, safranin, or rubin.

Bühler found the nuclei to lie generally nearer the end of the cell from which the process came off, frequently so close to the surface "dass er stellenweise die Zellgrenze zu bilden scheint" (p. 17). On the side of the nucleus toward the greatest cytoplasmic mass, and therefore opposite the nerve process where that is to be seen, appear from one to three small, intensely stained granules, lying close together, and sometimes connected by a "Substanzbrücke." About this granule or group of granules is a clearer area of cytoplasm, and there may be one or several more or less complete dark circles concentric about the central granules. Radial fibres often appear extending out from the central granules, sometimes only to the inner of the surrounding circles, and sometimes quite to the periphery of the cell. Each of these concentric circles is due to a series of varicosities on the radial fibres, at equal distances from the central granules. In some preparations, however, the radial fibres are not conspicuous, and the circles appear to be made up of rows of granules.

Other systems of fibres run more or less parallel to the cell surface, or concentric to the nucleus, and are traceable out into the processes. These fibres, which Bühler believes to be limited to the surface of the cell, also bear varicosities and appear to intersect the radial fibres, the points of intersection being marked by "kleine Knötchen." The central granules Bühler believes to correspond to the "Centralkörper" of Heidenhain, and the radial fibres to Heidenhain's "organische Radien."

As to the function of the centrosome in the resting cell, Bühler says (p. 37): "Wo, wie in reifen Ganglienzellen ihre Beziehung zur Zellteilung nicht nachgewiesen werden kann, da tritt ihre zweite Function in ihre Rechte: Sie sind in der ruhenden Zelle die Insertionsmittelpunkte für das centrirte Fibrillensystem." Bühler states (p. 38) his belief that "nicht nur das dynamische Centrum der Zellteilung in Gestalt der Centralkörper, sondern das gesammte System der organische Radien einschliesslich der Attractionssphäre dauernd in ruhenden Zellen sich erhält."

Dehler (**'95**) described structures in the sympathetic-ganglion cells of the frog very similar to those described by von Lenhossék for the spinal-ganglion cells of the same animal. Dehler, like von Lenhossék, obtained his best results with sublimate fixation and Heidenhain's staining methods. He found the nuclei excentric and lying at the end of the cell opposite the nerve process. They are generally flattened or concave on the side toward the cell centre. The cytoplasm contains "Schollen die sich concentrisch im Zellleib zu einander reihen." The centre about which the "Schollen" are arranged is approximately the centre of the cell. They are generally larger toward the periphery of the cell. The central region of the cell is more often quite free from them, and they are less marked, or even absent, in the smaller cells.

At the centre of the cell lies the "Centralkörpergruppe," composed of several deeply staining granules. About them the section of the cell exhibits a well-defined circular clear area from 5 μ to 7 μ in diameter. It is very finely granular and is bounded by neither a membrane nor a row of granules. In some of Dehler's figures there is about the central clear area a considerable zone free from the coarse "Schollen." In other cases the "Schollen" extend quite to the boundary of the clear area, which corresponds to von Lenhossék's "Sphäre." Dehler found no radiations from the region of the centrosome.

Flemming (**'95**^{a}) described a concentric arrangement of granules about the nucleus of the spinal-ganglion cells of mammals, but he found no structures similar to the centrosome and sphere which then had been recently described by von Lenhossék in the frog.

Schaffer (**'96**) described centrosomes in certain cartilage cells of Myxine glutinosa and also in nerve cells of the cranial ganglia of Petromyzon planeri 15.5 cm. long. His material was fixed in picro-sublimate and stained in hæmalum-eosin. Schaffer found cells with the nuclei excentric. The cytoplasm was very finely granular, and in it was commonly found a structure forming " eine Art von Gegengewicht im Protoplasma gegenüber dem Kern " (p. 26). These cytoplasmic structures appeared in some cases as merely small areas of irregular shape and varying size, staining red in contrast to the surrounding blue. Often two such areas of unlike form and size lay near together. In some cases a small clear space surrounded the darker area. In still other cells a circular clear area contained a small central granule, and at one side of the clear area lay an irregularly shaped red-staining mass similar to those found where no clear area and granule were present. Schaffer interprets the granule, clear area, and red-staining mass as centrosome, sphere, and archoplasm, respectively. He attributes the failure to find all three of the structures in so many cells to unfavorable planes of cutting, or to other causes. No radial arrangement of the cytoplasm was seen. He suggests that the structures described may be concerned in nuclear divisions of the ganglion cells, since he has often seen in Petromyzon ganglion cells with two nuclei.

McClure (**'96, '97**) described centrosomes and spheres in the nerve cells of Helix and thinks they may exist in Limulus. In Astacus, Cambarus, Homarus, Lumbricus, Arion, and Limax he failed to find these structures. In unipolar ganglion cells of Helix with a transverse diameter between 17 μ and 22 μ he finds excentric nuclei often flattened, or more frequently kidney-shaped. His figures show the nuclei lying at the end of the cell opposite the nerve process, and the flattened or concave side of the nucleus is never "directed exactly opposite to the base of the axis-cylinder process, but always to a point on one side of it." "In the body of the cell, directly opposite the invagination [of the nucleus], a disc-shaped structure was found." The disc is finely granular, but shows no radial arrangement. "Within these discs and at about their centre, two or three small granular bodies were present which stained much deeper than the surrounding granules and which I have taken for centrosomes." A zone of cytoplasm immediately surrounding the disc stains darker than the disc, because of a concentration of small chromophilous granules, but no radial arrangement among these granules is to be seen. The centrosome and sphere were best seen in material fixed in Flemming's fluid and stained in iron-hæmatoxylin. Sublimate preparations with the same stain gave confirmatory results. In some cases, large spherical pigment granules were found arranged in a circle just outside the disc and close to its boundary.

Miss Lewis (**'96**, **'98**) described the presence of a centrosome and sphere in the giant nerve cells of Clymene producta. She demonstrated the presence of these structures by the use of vom Rath's picric-osmic-acetic-platinic chloride mixture, not followed by a stain. Sublimate fixation followed by Heidenhain's iron-hæmatoxylin gave confirmatory results.

The nucleus of these giant cells is excentric and flattened or concave on the side toward the cell centre. The sphere is a more or less sharply defined region lying near the cell centre and has a diameter about one-third that of the cell. It consists of an outer "broad zone of coarsely granular protoplasm; within this a smaller area of more nearly homogeneous protoplasm; and in the centre of this a very small highly refractive body, or occasionally two or three such bodies." The central bodies sometimes have the form of short rods. From the central granule, or granules, radiations "traverse both the inner, more homogeneous zone and the outer, coarsely granular zone. Sometimes the radiations pass even beyond this into the surrounding, finely granular protoplasm of the cell" (**'96**, p. 296). The radiations are composed of minute granules arranged in radiating lines.

Dahlgren (**'97**) examined spinal-ganglion cells of the dog and found appearances which resembled centrosomes and "centrospheres," but which he believed to be artifacts due to the crystallization of corrosive sublimate. The questionable structure, always found between the pigment mass and the nucleus, appeared in the section as a disc free from granules and having at its centre a black spot. Focussing revealed a radial arrangement of the disc, and the surrounding cytoplasm showed a "distinct concentric arrangement."

In some twenty-five cells, before the sublimate had been dissolved out by means of iodine, Dahlgren observed radiating crystals of the sublimate occupying the region where, in the same cells after staining, the supposed artifacts were seen.

That the crystals should always be found at the same region of the cell, Dahlgren says, "would indicate some difference in the constitution of the cell at this point."

Dogiel (**'97**, p. 108) mentions that, in methylen-blue preparations of the spinal-ganglion cells of certain mammals, "in einer gewissen Entfernung vom Kerne ein runder oder ovaler heller Fleck mit einem kleinen, von Methylenblau stark gefärbten Körnchen im Centrum zu bemerken war." This is probably, he thinks, the centrosome and sphere described by von Lenhossék.

Heidenhain und Cohn ('97) find the "Microcentrum" in the cells of most of the tissues of bird embryos. In the cylindrical cells of the neural tube the microcentres lie at the extreme outer ends of the cells. In a surface view of a group of these cells their outlines form a polygonal network, "dessen Maschen die übrigens nicht regelmässig central gestellten Microcentren, je eines in einem Zellenterritorium, einschliessen. . . . Findet man in einem bestimmten Zellenfelde das Microcentrum nicht vor, so ist man häufig in der Lage zu konstatiren, dass in dem zugehörigen Zellenkörper eine Theilungsfigur enthalten ist, dass somit die Centralkörper zum Zwecke der Mitose in die Tiefe der Epithelzelle eingerückt sind" (p. 205).

Bühler ('98) finds excentric nuclei in cells of the spinal ganglia of Bufo vulgaris. In the cytoplasm chromophilous flakes, which are larger toward the periphery of the cell and smaller toward the centre, are arranged in concentric order about a point lying near the cell centre. Certain fibres also participate in this concentric arrangement. Close to the nucleus and on the side toward the cell centre lie two minute granules staining deeply in hæmatoxylin and connected by a dark band. About these as a centre are one or two rows of similar but less conspicuous granules arranged in arcs of circles. Extremely fine radiations pass outward from the central granules; they intercept in their courses the granules of the concentric arcs and are sometimes capable of being followed quite to the cell periphery. Granules staining in hæmatoxylin occur at rather regular intervals along the course of a fibril. *The concentric arrangement is about the approximate cell centre and not about the granules at the centre of the radiating system.* The latter centre lies in the line passing through the centre of the nucleus and the centre of the cell as a whole, — the principal axis, as determined by Heidenhain, — but toward the nucleus end of the cell from the cell centre. The "Microcentrum" described by Heidenhain for leucocytes lay at the cell centre. Bühler says (p. 49): "Bei mehreren Centralkörpern gelang es mir fast immer, eine Verbindung in Gestalt eines dunklen Bandes, die primäre Centrodesmose Heidenhain's zu sehen." The system described by Bühler corresponds, therefore, to the "Microcentrum" and "organische Radien" of Heidenhain.

The results, then, of the work of von Lenhossék and Bühler upon the same material, the spinal-ganglion cells of the frog, are at considerable variance. They agree in showing a concentric structure in the cell body, but von Lenhossék finds the centrosome at the centre of the concentric structure, while Bühler finds his "Centralkörper" near the nucleus and remote from the centre of the concentric arrangement. Von Lenhossék's centrosome is composed of a large number of granules; Bühler finds generally only two granules composing his "Centralkörper." In the toad and other vertebrates, including mammals, Bühler finds radiations from the "Centralkörper;" von Lenhossék described no radial structures. Bühler, in the paper referred to ('98), compares critically his results with those of von Lenhossék and other authors.

Bühler states that structures similar to those described by him ('95) in the brain of the lizard he has seen also in some of von Kölliker's Weigert preparations of pyramid cells from the human brain, and likewise in Cohn's preparations of nerve cells from an adult mouse.

Hunter ('98) noticed that van Beneden et Julin ('84), in a work on the central nervous system of ascidians, represented excentric invaginated nuclei in the nerve cells of Molgula. He consequently was led to investigate the cells of the central nervous system of Cynthia partita, and found the nuclei always excentric and generally at the end of the cell opposite the process. The form of the nuclei varied from spherical to cup-shaped. Occupying the centre of the cell was a structure which he considered homologous to the centrosome and sphere of von Lenhossék. At the centre of a "clearly staining area, homogeneous or finely granular," were one or several "black deep-staining granules, the centrosome or central bodies of authors." Surrounding the clear area was a coarsely granular zone of varying diameter. In some cells were "well developed astral rays, presenting the appearance found in leucocytes."

There were many modifications of the structure. In some cells all the parts mentioned were found, while in others only a central deeply staining granule was found with no definite cytoplasmic arrangement about it. In very young animals killed shortly after metamorphosis a larger proportion of cells showed the structure than in the adults. In these young cells the sphere and radiations were generally lacking, or at most only a very narrow clear area with a slight condensation about it was found. There were generally two central granules. In the cells of the young Cynthia the nuclei were excentric but rarely invaginated, and the centrosomes seemed to have no fixed position in the cell body, often being found "laterally between the nucleus and the cell membrane." Speaking of the absence of sphere and radiations in the young cells, and the varying position of the centrosomes, Hunter says: "These facts can only be explained on the supposition that the centrosome does not exert any decided mechanical influence on the cell protoplasm."

Hunter found individual variation as to the frequency of the presence of the centrosome in the nerve cells of different animals killed at the same time, the preparations being subjected to exactly the same treatment throughout.

Rohde ('98) finds that certain "Nebennucleolen" wander out from the nuclei into the cytoplasm of nerve cells of the frog, and come to resemble closely the sphere described by Dehler. In the cytoplasm of the nerve cells of the dog he found bodies of nucleolar origin.

In nerve cells of the frog, Rohde commonly finds structures that resemble a "centrosphere." They consist of a central dark body in a clear area, which lies within a sphere exhibiting a radial arrangement. The whole structure suggests the centrosome and sphere described by von Lenhossék. Rohde, however, maintains the existence of such structures in all the cells of the ganglia, — not merely in cells of a certain size, as described by von Lenhossék, — and in any region of the cell whatever, even within the nucleus, or immediately outside the cell body. Moreover, as many as eight of them may occur in one cell. They were not found in the cells of mammals. Rohde thinks they are not artifacts. As regards the existence of the centrosome in the nerve cells of either invertebrates or vertebrates, he says, "Centrosomen kommen also bei Ganglienzellen nicht vor."

Hamaker ('98) found structures in the nerve cells of Nereis which he considered to be comparable to the centrosomes described for nerve cells by other authors. Often two or three of these structures and sometimes as many as ten were found in a single cell. Each one consisted of a deeply stained granule in a clear space enclosed within a hollow sphere of coarse granules. No radiations were seen. The nuclei were excentric and often flattened. The "centrosomes" lay at the centre of the cell body.

Holmgren ('99) occasionally finds sections of cells which exhibit a central structure very similar to the sphere of von Lenhossék. He describes a system of fibres which sweep in from the periphery of the cell to form a "Spiralfigur." Similar conditions are described by Bühler ('98). Among the generally hyaline fibres of this system are some more deeply staining fibres. Holmgren thinks certain favorable sections through this spiral system give the appearances interpreted by von Lenhossék as a sphere, his "centrosomes" being simply sections of some of the deeply stained fibres that happened to lie at the centre of the spiral figure.

Kolster ('00) gives a brief preliminary account of centrosomes in the nerve cells of Cottus scorpius. The only two figures given represent one or two deeply stained granules surrounded by a small clear area and lying near the cell centre, the nuclei being excentric and concave on the side toward the cell centre.

2. The Centrosome in Other Resting Cells.

Leaving nerve cells and turning now to the question of the centrosome in other resting cells, and especially in tissue cells, a considerable literature on this subject is found to have grown up during the last ten years. Previous to 1889 no accurate description had been given of a centrosome and sphere in resting tissue cells, but doubtless many of the descriptions of "Nebenkerne" and "Centralmassen" refer to structures that would now be recognized as centrosomes or spheres.

Van Beneden et Neyt ('87, p. 279) found that the attraction sphere persisted during the resting periods of the early cleavages of Ascaris. "Nous sommes donc autorisés à penser que la sphère attractive avec son corpuscule central constitue un organe permanent, non seulement pour les premiers blastomères, mais pour toute cellule; qu'elle constitue un organe de la cellule au même titre que le noyau lui-même; que tout corpuscule central dérive d'un corpuscule antérieur; que toute sphère procède d'une sphère antérieure, et que la division de la sphère précède celle du noyau cellulaire."

Boveri ('88) showed the continuity of the centrosome in the cleavage of Ascaris, and set forth his conception of a specific "archoplasm," which is strewn through the cell in granular form during the resting period, and, in mitosis, collects about the centrosomes to give rise to the radiating systems.

Rabl ('89) observed that the resting nuclei of epithelial cells in Triton were indented upon one side, while in the cytoplasm, in the region of the indentation, was a highly refractive homogeneous mass which, he suggested, was due to the presence of the "Polkörperchen" or the "Attractionssphäre."

Solger ('89, '90) found a radiating structure in the pigment cells of some teleosts. The cells frequently have two nuclei which are situated at the cell centre, and between them is a small clear area, from which proceed radiating lines of granules toward the periphery. The central area Solger suggests to be "das Centralkörperchen oder die Sphère attractive im Ganzen oder ein Theil derselben."

Kölliker ('89) found the attraction sphere in cleavage cells of Siredon while the nucleus was in the resting condition.

Bürger ('91) found an attraction sphere with centrosome and radiations in the cells of the body fluid of nemertines.

Flemming ('91, '91[a], '91[b]) described "die strahligen Sphären und ihre Centralkörper" in resting leucocytes of the salamander. In the amitotic divisions of the nuclei of these cells the sphere does not divide, but Flemming believes that it exerts some influence over the amitotic process, since "bei den Abschnürungen die Sphäre eben nicht einer beliebigen Stelle der Kernmasse benachbart liegt, sondern grade an den Abschnürungsbrücken" ('91[a] p. 285). The centrosome was also found in the resting cells of the lung epithelium and in the flat connective-tissue cells and endothelial cells of the peritoneum of the salamander larva, but in these fixed cells no radiations could be seen. The "Centralkörper" generally consisted of two minute granules lying close together in the cytoplasm very near the nuclear membrane. Often a dark band could be seen connecting the two granules. When the nucleus was approaching the spireme condition the centrosomes were farther apart and this dark band was more conspicuous. Flemming therefore believed it to be "die erste Bildungsanlage der Spindel."

Flemming's discovery, made on leucocytes of the salamander, was corroborated by Heidenhain ('91), who also found the centrosome and sphere in the cells of the bone-marrow of young rabbits, as well as in pathological epithelium from human lungs and in some leucocytes from the same human material.

Henneguy ('91) showed the continuity of the attraction spheres in the developing trout egg.

Hermann ('91) found an "Archoplasmastrahlung" in resting spermatogonia of the frog, and resting spermatocytes of Helix pomatia. In resting spermatocytes of Proteus he describes an archoplasm with a conspicuous central granule.

Meves ('91) described amitosis in the spermatogonia of the salamander. During the dividing of the nucleus the "attraction sphere" took the form of a ring about the region of constriction.

Solger ('91) described an attraction sphere in resting chromatophores of teleosts.

Heidenhain ('92) observed, in two cases of leucocytes with two nuclei, two spheres present, with a well-developed spindle formed between them.

Generally the leucocytes had a single sphere, even though more than one nucleus may have been present.

Vom Rath (**'92**) found amitotic conditions in the "Stützzellen" of the testis of Gryllotalpa. He says, "Es gelang mir mehrfach in unmittelbarer Nähe der Kerne zwei winzige Centrosomen zu erkennen und ebenso constatirte ich in seltenen Fällen bei eingeschnürten Kernen eine deutliche Strahlung um die beiden Centrosomen, die offenbar als Attractionssphäre bezeichnet werden muss" (p. 115).

Van der Stricht (**'92**) showed the continuity of the attraction spheres in the cleavage of Triton. He also showed that the centrosomes of mitosis in cartilage cells of various vertebrates persist in the resting cell.

Brauer (**'93, '93**^{a}) discovered the centrosome *within* the resting nucleus of spermatocytes of Ascaris megalocephala univalens. Preceding a division of the cell, the centrosome divided while inside the nucleus and the two resulting centrosomes migrated into the cytoplasm.

Moore (**'93**) described an archoplasm with a "central body," "medullary zone" and radiations in resting cells of the undifferentiated genital ridge of the larval salamander. The archoplasm gave rise to the spindle of mitosis. In leucocytes of the larval salamander a similar structure was found, instead of the simpler conditions described by Flemming (**'91**).

Vom Rath (**'93**) described attraction spheres and centrosomes in various resting cells of Amphibia and studied the behavior of these structures during amitosis of the sexual cells. The structures were found also in the sexual cells of Astacus.

Watasé (**'93**, p. 442) concludes that "the *centrosome* is not a unique organ of the cell, but is identical with the *microsome* which exists everywhere in the cytoplasm."

Zimmermann (**'93**) described what he considered to be a modified attraction sphere in pigment cells of teleosts. There is a very much elongated "Centralstab," comparable to a centrosome, imbedded in a correspondingly elongated "Archiplasm," whence proceed radiations. In certain very large cells the radiations proceed from a "Centralnetz" instead of from a "Centralstab." In the smaller cells a spherical "Archiplasm" with radiations and a minute centrosome were present.

Heidenhain (**'94**) investigated, in great detail, the conditions in leucocytes and other cells of vertebrates. The "Microcentrum," which he finds generally present, consists of two or three granules imbedded in an achromatic "Centrodesmose," which he believes gives rise to the spindle. The microcentre is the point of insertion of a system of radiating fibres, which extend to the periphery of the cell. These fibres, according to Heidenhain, are contractile and in a state of tension, which is a source of energy displayed in the mitotic processes. The microcentre lies at the centre of an astrosphere, which is bounded by a layer of microsomes occurring on the radial fibres at equal distances from the centre. The astrosphere is not an organ of the cell, but only a region which takes a characteristic stain because of the concentration of the radial fibres.

In the giant cells of bone-marrow, which have polymorphic nuclei, mitosis occurs without a division of the cell body. In these cells several groups of "Centralkörper" were found, each group containing many granules.

Heidenhain predicted that the microcentre with its radiating system would be found in most resting cells.

Reinke (**'94**) found the centrosome and sphere in leucocytes of the salamander. Leucocytes of amœboid form differed from those of resting form in having coarser radiations of unequal thickness and thickenings of the fibres arranged in arcs concentric about the centrosome.

Dehler (**'95^a**) described a microcentre (Heidenhain), without radiations, in the red blood corpuscles of the chick embryo. He believed the microcentres to be derived from the centrosomes of mitosis.

Drüner (**'95**) observed centrosomes in the resting sperm cells of the salamander and in resting cells of the gastrula of Triton alpestris. He gives an extended criticism of Heidenhain's mechanical theory of the centred system and sets forth an opposed theory. Drüner believes that the radiations of the resting cell disappear before a mitosis and that new radiations arise from the centrosomes. He divides the mitotic process into two periods, the first ending with the division of the chromosomes in the equatorial plate. "Die erste Periode ist die der Expansion, die zweite die der Kontraction des gesammten Strahlensystems" (p. 333).

Niessing (**'95**) found the centrosome with sphere and radiations in the liver and spleen cells of the salamander and in the liver of the human embryo.

Vom Rath (**'95^a**) described a centrosome and sphere in the large gland cells of the head of Anilocra mediterranea; also in the hepatopancreas cells of Porcellio scaber and in spleen cells of a young dog. In amitotically dividing leucocytes and sperm cells there are sometimes one and sometimes two centrosomes and spheres. Vom Rath concludes "dass eine Theilung der Attractionssphäre bei der Amitose stattfinden kann . . .; ob sie aber immer stattfinden muss, ist unwahrscheinlich" (p. 61).

Von Erlanger (**'96**) observed the centrosome in resting epithelial cells of salamander larvæ. There were always two, connected by a band of substance. In mitosis these centrosomes moved apart and the spindle formed between them. In another paper (**'96**^{a}) he describes a "Nebenkern" in resting sperm cells of the earthworm. In rare cases a central granule and weak radiations were present. He believed the structure to be archoplasm and centrosome.

Meves (**'96**), in the spermatogonia of the salamander, found the spheres of adjacent cells connected by bands of substance which are probably remnants of the spindle.

Ballowitz (**'97**^{a}) demonstrated the centrosome and sphere in the cells of the pharyngeal and cloacal epithelium of Salpa, without the use of stains. The material was fixed in either weak or strong Flemming's fluid, sublimate, or acetic-sublimate, and examined in water. The nuclei are sickle-shaped, and in the concavity of each could be seen the large sphere which Ballowitz had previously described (**'97**). A detailed study of the epithelial cells of Salpa appeared in a later paper (**'98**^{a}). The centrosomes were best seen in the unstained Flemming's preparations. At the centre of the sphere were generally two, but sometimes three or four, very highly refractive bodies. They often appeared to be irregularly shaped or elongated, instead of spherical granules. Ballowitz concludes "dass es zum Nachweise der Centrosomen nicht immer einer specifischen Färbung bedarf, dass diese wichtigen Zellbestandtheile vielmehr auch in ungefärbtem Zustande in Folge ihres charakteristischen starken Lichtbrechungsvermögens so scharf begrenzt hervortreten, dass sie leicht und sicher in der Sphäre erkannt und unterschieden werden können" (p. 358).

Ballowitz believes the sphere and centrosomes to be present also in the epidermal cells of Amphioxus larvæ (**'98**). These cells have nuclei varying in form from those that are deeply invaginated to those that are sickle-shaped or complete rings.

Eisen (**'97**) described a new element found by him in the blood of some amphibians, reptiles, and man. To this element he gave the name of "plasmocyte." He attempts to show that the plasmocytes "are composed of the centrosomes and archoplasm (with part of the cytoplasm) of the nucleated erythrocytes, . . . surviving in the blood serum as free and independent elements capable of growth through assimilation of food, and taking their place as blood elements, equal in importance to the erythrocytes and leucocytes" (p. 13).

Von Lenhossék ('98), in studying the development of the spermatozoa of the rat, found the flagellum to be a product of the centrosome. In another paper ('98ᵃ) he described the centrosomes and "Basalkörperchen" in the cells of ciliated epithelium. In cells that did not bear cilia, the microcentre was present, lying at the extreme outer end of the columnar cell. In the ciliated cells no microcentres were found, but there was a layer of granules just beneath the ciliated surface of the cell, the number of granules corresponding closely with the number of cilia. Von Lenhossék gives the name of "Basalkörperchen" to these granules, and thinks they are homologous with the microcentre of the non-ciliated cells.

Zimmermann ('98) discusses the centrosome in epithelial and gland cells of mammals, including man. He points out that, as in mitosis the centrosome is the centre of motor processes, so in resting cells the centrosome is always located at the centre of activity. If there is an equal degree of activity throughout the cell, the centrosome is at the centre of the cell, unless displaced by a large nucleus (leucocytes, pigment cells, non-striated muscle cells). In gland cells, it is at the centre of secretory activity. In ciliated cells and epithelial cells with pseudopodial processes, the microcentre is close to the outer end of the cell. Where there is a single flagellum, as in the spermatozoön, the centrosome is at the point where the flagellum enters the cell. He says (p. 697): "Ich glaube . . . dass, ganz allgemein gesprochen, das Mikrocentrum das motorische Centrum, also das 'Kinocentrum' der Zelle sei (gegenüber dem Kern als 'Chemocentrum')."

Von Lenhossék ('99) describes a microcentre, in the sense of Heidenhain, in the non-striated muscle cells of the cat. As non-striated muscle cells are known to divide by mitosis in cases of regeneration, we should expect to find the microcentre in the resting cell.

Among other authors who have described centrosomes in resting cells may be mentioned Hansemann ('91, '93; cells of human brain tumor, cancer cells, human leucocytes, mesenterial connective tissue of young cats and rabbits); Guignard ('91, '97; plant cells); Eismond ('94; cleavage cells of Triton tæniatus and Siredon); Zimmermann ('94; human epithelium, stroma cells of cat ovary); de Bruyne ('95; connective-tissue cells); Meves ('95; spermatogonia of salamander; '95ᵃ; sesamoid cartilage cells in the tendon achilles of the frog); Moore ('95; sperm cells of elasmobranchs); Rawitz ('95; sperm cells of salamander); Gulland ('96; leucocytes); Spuler ('96; connective-tissue cells); Child ('97; ovarian stroma cells of mammals); Heidenhain ('97; red blood corpuscles of duck embryo); Rawitz ('98; sperm cells of Scyllium canicula); Niessing ('99; lymphocytes).

Reviews of the centrosome question, with lists of literature, have been given from time to time by various authors, among them Flemming ('93), Moore ('93), Häcker ('94), Heidenhain ('94), vom Rath ('95), Henneguy ('96), von Erlanger ('97), Heidenhain ('97), Kostanecki und Siedlecki ('97), Bühler ('98; centrosome in nerve cells), and Meves ('98).

III. Methods of Investigation.

The identity of the so-called centrosome of nerve cells with the centrosome of mitosis can be established by a series of observations showing that the centrosome of the last mitosis of the embryonic nerve cell persists through the development of the nerve cell and becomes the structure seen in the resting cell; or, if the cells can be induced to divide by mitosis, it may be possible to show that the centrosome of the resting cell gives rise to the centrosomes of the mitotic figure. The problem, then, is open to attack from two directions. Given, material in which the presence of a centrosome in the differentiated nerve cells can be demonstrated, — as it has been in many vertebrates and invertebrates, — and in which the centrosome is also to be found in the embryonic neural tissues, — as Heidenhain und Cohn ('97) have found it in the neural epithelium of bird embryos, — then we may seek to establish the genetic relationship of the organ in the embryonic cell with that of the differentiated cell.

A second method of investigation is offered by the process of regeneration. If any cells of adult nervous structures are capable of undergoing mitotic division, regeneration would seem to offer the most favorable opportunity for the exercise of such power. If, however, the regenerated nerve cells do not arise from old nervous tissues, the development of the new nerve cells from other tissues would still offer opportunities for determining whether the "centrosome," if present in the regenerated cells, had persisted from the last mitosis in the history of the cell.

The question arises as to whether processes which take place in the *embryonic* origin of nerve cells will be repeated in the *regenerative* development of similar cells. To show that a centrosome in a regenerated nerve cell is one of the centrosomes of the mitosis of the mother cell, does not necessarily prove that the centrosome of a nerve cell which has arisen by the natural embryonic process of development is also identical with a centrosome of the mitosis of its parent cell. Yet, if the regenerated nerve cells arise from ectodermal tissues, we should certainly expect the processes of regenerative development to resemble very closely those of embryonic development, especially in so fundamental a thing as the fate of mitotic organs. Many investigations have shown the similarity of regenerative and embryonic processes. If it is shown that the "centrosome" of a regenerated nerve cell is a true centrosome, — that is, the organ concerned in mitosis, — it must be admitted as highly probable that the similar organ in the naturally developed cell is likewise a true centrosome.

In an investigation upon any one kind of material, the regenerative process has an advantage over the embryonic, for it affords not only the opportunity for the study of the development of nerve cells, but also the possibility of observing whether the structures under consideration in the already differentiated nerve cells have anything to do with the formation of new cells.

The observations about to be described have been made upon tissues in process of regeneration, the object being twofold, — to determine, first, the behavior of elements in old nervous structures in the presence of the necessity for regeneration; and, secondly, the source and method of development of the new nervous parts.

1. Material.

Two qualities were demanded of material intended for this work. The fully differentiated nerve cells must contain some such structure as has been called a centrosome by various authors, and the animal must have the ability to regenerate excised parts of the nervous system. It was at first proposed to work upon the annelid, Axiothea (Clymenella) torquata. In the giant cells of a nearly allied form, Clymene producta, Miss Lewis (**'96, '98**) found the centrosome and sphere to be present. I found some evidence of a centrosome in the giant cells of Axiothea, but nothing as definite as Miss Lewis demonstrated for Clymene. Axiothea was found to regenerate segments very readily at either the anterior or posterior end. I obtained regeneration in a large number of the worms during the summer of 1898, at the laboratory of the United States Fish Commission at Wood's Hole. A number of segments having been cut from either or both ends, the worms were placed in glass vessels partly filled with clean sand over which ran sea water. In the course of two to four weeks a considerable regeneration was found to have taken place at the cut ends. Two facts caused this material to be abandoned. The centrosome in the giant cells was too indefinite a structure to deal with satisfactorily, while the very limited number of giant cells in a segment made the prospect of obtaining a comprehensive series of conditions in the regenerative development of these cells anything but encouraging.

Hamaker ('98) demonstrated some centrosome-like structures in the nerve cells of Nereis. I made preparations of Nereis and found some very decided evidence of the presence of the centrosome in the cells of the ventral ganglia (page 115). At the same time I examined nerve cells of the earthworm, obtaining results which inspired further investigation of that material. This fact, together with the well-known regenerative power of the earthworm and the greater ease of conducting regeneration experiments upon the land annelid, determined its use for this work in preference to Nereis. It is, therefore, mainly with the earthworm that the following work has to do.

2. Regeneration Methods.

The worms, Allolobophora (terrestris Savigny ?) and Lumbricus agricola Hoffmeister, were easily obtained near the laboratory in Cambridge. From five to ten segments were removed from the anterior end, and the beheaded worms were placed in large earthen jars filled with the soil in which the worms were found. The soil was first carefully examined and all other worms removed. Most of the regeneration was obtained during the winter or early spring months. The jars were kept in the vivarium at a temperature of about 16° C. The earth was moistened from time to time so that it never became dry at the surface. Many of the beheaded worms burrowed a short distance below the surface, but many others refused to burrow and persisted, if buried under a little earth, in returning to the surface. To protect them from the light and from drying, sheets of moistened filter paper were spread over the surface of the earth and the jars were covered with glass plates.

The cutting of the anterior end prevented feeding. In the course of a few days the intestine of the worm was entirely free from earthy material. The smaller worm, Allolobophora, generally burrowed beneath the surface and coiled itself into an intricate close knot, remaining in that condition, unless disturbed, as long as it was kept, — five or six weeks. The larger earthworm, Lumbricus, which generally remained on the surface, was always found stretched out when the earth was exposed for moistening.

An attempt was made to keep some worms during regeneration in glass vessels containing moist filter paper, instead of in earth; but the method was more troublesome and possessed no advantages over the other. Unless the paper was changed every day or two, the worms were likely to die, while of those kept in the earth only about ten per cent died during regeneration.

Worms were killed after from seven to forty days subsequent to the operation. In Allolobophora, the light-colored conical bud that marked the regenerated segments was usually to be seen in two or three weeks after the operation of cutting. Lumbricus regenerated much more slowly. All of the preparations which I shall discuss are from individuals of Allolobophora.

Regeneration of posterior ends was also obtained, but little was done upon that material. The anterior ends have the advantage that the regeneration of both the brain and ventral nerve-cord can be observed.

When the desired period of regeneration had elapsed, the worms were dropped into fresh water for a moment to remove the clinging earth. The anterior end, including some six to twelve of the old segments, was clipped off with scissors and the fragment bearing the regenerated part was at once dropped into the fixing fluid. Stupefaction, where such small fragments were to be fixed, was found to be of no advantage.

In the less advanced stages of regeneration the inability to feed made unnecessary the cleaning out of the intestine before fixing. In some of the more advanced stages feeding had been resumed and the worms had to be kept upon moist linen for a day or two until the anterior part of the intestine had become clean.

3. Fixing Fluids.

The best fixing fluid for general purposes was found to be Flemming's stronger chromic-osmic-acetic mixture. This fluid not only gave the best fixation of the old ganglion cells, but also gave by far the most satisfactory fixation of mitotic cells. Some of the best demonstrations of the exceedingly fine radiating fibrillæ in the ganglion cells were obtained by this method, and the achromatic fibres of the mitotic figure were very sharply brought out.

Material was left in the fixing fluid for from five to forty-eight hours. A longer or shorter time within these limits gave no appreciable difference in results. The objects were then washed in distilled water for about twenty-four hours, then passed through ascending grades of alcohol, cleared in cedar oil and imbedded in paraffin.

Hermann's acetic-osmic-platinic chloride mixture was used with good results, although it seemed to be in no way superior to the Flemming mixture. The Flemming preparations gave a rather better quality of stain with Heidenhain's iron-hæmatoxylin. The method of treatment with Hermann's fluid was similar to that just described for Flemming's fluid.

Vom Rath's picric-osmic-acetic-platinic chloride gave no results of value. The after treatment with crude pyroligneous acid was used as described by vom Rath ('95). In some cases a two per cent solution of pyrogallic acid was substituted for the pyroligneous, with similar results. The length of time of the after-treatment, during which the reduction of the platinic chloride takes place, was varied, but in all cases the cytoplasm was blackened to such an extent that it became too opaque for the observation of the exceedingly delicate structures revealed by other methods. In some preparations mitotic figures were brought out with remarkable clearness by this method, especially as to the sharpness of spindle fibres, but, for the observation of polar and cytoplasmic structures, fixation in Flemming's or Hermann's fluid followed by a regressive stain gave results far superior to those obtained by a method which depends upon the deposition of a metallic salt in the cell structures.

Corrosive sublimate in a saturated aqueous solution containing one per cent of acetic acid was used with results which corroborated those obtained by the Flemming and Hermann fluids as to cytoplasmic structures in the ganglion cells, but the demonstration of these structures was far inferior to that obtained by the other methods. The sublimate failed to bring out the finer structure of the cytoplasm as clearly as the osmic mixtures. Radiating fibres were very indistinctly shown. The sublimate gave decidedly inferior results in the demonstration of mitotic figures. My preparations lead me to believe that the sublimate effects violent mechanical injuries in delicate tissues. In such solid tissues as the epidermis or intestinal epithelium there were no evidences of injurious effects; but among the very loosely aggregated masses of cells that constitute some of the regenerated parts, there were signs of serious damage. In the epidermis, for example, spindle figures occur imbedded in a dense cytoplasmic mass. These figures were faithfully preserved by the sublimate. In the regenerating brains and ganglia, the mitotic figures more often occur in cells the remaining contents of which appear to have become entirely fluid. Such figures, unsupported by a dense cytoplasm and completely exposed to the action of the fixing fluid, were very seriously distorted in the sublimate preparations. In all cases spindle fibres were very poorly shown in the sublimate preparations.

As for the superiority of Flemming's fluid for the demonstration of the centrosome, my experience agrees with that of Ballowitz (**'97**^{a}, p. 358) who demonstrated centrosomes in epithelial cells of Salpa without the use of stains. He succeeded in doing this with sublimate, but Flemming's fluid gave by far the best results. He says, "Ich behaupte auf Grund meiner Erfahrungen an meinem Untersuchungensobject, dass es mit grösserer Sicherheit und mehr Constanz gelingt, die Centrosomen an dem mit Flemming'scher Lösung fixirten, ungefärbten Material zu erkennen, als durch specifische Tinction an den mit Sublimat behandelten Objecten sichtbar zu machen."

My Flemming preparations were all stained with iron-hæmatoxylin, but they were decolorized to such an extent that, examined by a low power, the cell bodies appeared scarcely darker than in the unstained preparation. But examination with high power revealed the fact that the cell granules had retained the stain. It was in such preparations that central granules were most clearly seen, because of their deep stain in contrast to the unstained ground substance of the cytoplasm. Hermann's fluid gives substantially the same results in this respect. I have examined unstained Hermann's fluid preparations and have been able to distinguish fairly well the granules and fibrillæ of the cytoplasm. In stained sublimate preparations there is apt to be present in the cytoplasm a large amount of deeply staining material scattered about in irregular masses, obscuring finer details of structure. If the decolorizing is carried so far as to clear out these masses, the granules and fibrillæ are left much less distinct than in the decolorized osmic acid preparations.

All the material was cleared in cedar oil and imbedded in paraffin. Sections were cut generally $6\frac{2}{3}\ \mu$ thick. A few series were cut at $3\frac{1}{3}\ \mu$.

4. STAINS.

Heidenhain's iron-hæmatoxylin proved to be by far the most useful stain. Sections were treated with a two per cent solution of iron-alum from three-quarters of an hour to three hours and stained about the same length of time in a one-half per cent solution of hæmatoxylin. Decolorization was effected by the two per cent mordant, the process being controlled under the microscope.

This stain gave the best results both for the structure of the nerve cells and for mitotic figures in the regenerating tissues. No advantage was found to be gained by using safranin in combination with the hæmatoxylin. From what has been said, then, it follows that fixation in Flemming's mixture, followed by the iron-hæmatoxylin stain, proved to be the best combination.

Gentian violet was used to obtain sharp selection of kinetic chromatin, but it was useless for finer cytoplasmic structure. Kernschwartz gave results similar to those obtained by the iron-hæmatoxylin, but inferior in clearness. One sublimate series was stained in Kernschwartz and safranin with fairly good results, especially as to some cells of the regenerated epidermis (Figures 44 and 45).

Whatever the stain used, the best demonstration of the "centrosome" and cytoplasmic fibrillæ was obtained when the stain had been well extracted from the cytoplasm. In heavily stained cells the finer structures were made out with much greater difficulty.

5. Drawings.

The preparations were studied with a Zeiss $\frac{1}{18}$ oil immersion and Zeiss achromatic oculars 3 and 4. The drawings were made with the aid of an Abbé camera. Attention is called to the fact that all the drawings of cells and mitotic figures are to the same scale, a magnification of 2000 diameters. The outlines of cells, nuclei, and nucleoli were traced with the aid of the camera. Generally the "centrosome" and prominent granules could also be located, but only in rare cases could the radiations represented in the figures be seen with the camera in place. The figures are reproduced from pencil drawings.

A diagrammatic treatment of the drawings was avoided as far as possible, and it was attempted rather to reproduce, as accurately as could be, the appearances seen in the preparations. The drawings were reproduced by the heliotype (gelatine) process because by it a more accurate reproduction of the relative conspicuousness of the structures represented in the drawings may be obtained than by the lithographic process. It must be understood, however, that in the figures of nerve cells the conspicuousness of the radiating systems is slightly exaggerated. These lines catch the eye more readily in the printed figures than they do in the preparations. In most cases it required the most careful focussing and varying of illumination to bring out the less distinct radiating fibrillæ.

IV. Observations.

1. The Nerve Cells of Lumbricidæ.

My first study to ascertain the condition of the nerve cells of the earthworm was made upon normal unregenerated material fixed in sublimate and stained in iron-hæmatoxylin. Some evidences of concentric and radial cytoplasmic structure were found, suggesting the presence of structures which might be brought out more clearly by better methods.

In transverse sections of the ventral ganglia the greater number of ganglion cells are cut in planes parallel to their long axes. The cells are situated ventrally and laterally in the cord. They are unipolar and pear-shaped, the larger ends being peripheral, while the processes extend dorsally and centrally. The nuclei, with extremely rare exceptions, are situated in the process end of the cell, often so far toward that end that the nuclear membrane is tangent to the tapering sides of the cell. The diameter of the nuclei varies from $6\,\mu$ to $16\,\mu$. The cells are from $22\,\mu$ to $60\,\mu$ in length, and from $10\,\mu$ to $28\,\mu$ in transverse diameter.

The nuclei are always nearly or quite spherical and *never invaginated.* In the resting nerve cells of many animals where the centrosome has been found the nucleus has been described as invaginated, the centrosome occurring in the cytoplasm on the invaginated side of the nucleus. The position of the nuclei in the nerve cells of the earthworm is such as to leave by far the greater mass of cytoplasm on that side of the nucleus opposite the nerve process.

Early in my study of these cells I was impressed with the fact that, in a large number of them, more or less irregular small masses of deeply stained material occurred near the nucleus and on the side of it toward the centre of the cell. If a line through the centre of the nucleus and the centre of the cell be called the axis of the cell, these masses occurred in or near the cell axis. Occasionally faint radiations could be detected coming from the region of the central masses just mentioned and extending toward the periphery of the cell.

A more careful study of later and more favorable preparations demonstrated the common occurrence, in the cells of the brain and ventral ganglia, of such cytoplasmic structures as are represented in Figures 1–9.

Figures 1, 2, and 3 represent cells from the subœsophageal ganglion of a normal worm, — that is, one that had not undergone regeneration. These cells are from a preparation which was fixed in strong Flemming's fluid for forty-eight hours and stained in iron-hæmatoxylin. The cells are typical unipolar nerve cells, lying in the ventral anterior region of the ganglion, with their processes extending dorsally. Figure 4 represents a cell from the dorsal posterior border of the brain of the same animal.

a. The Nuclei.

The nucleus of the nerve cell has a characteristic appearance. In osmic acid preparations it is nearly always spherical, or departs only slightly from that form, as in Figures 2 and 4. In sublimate preparations, however, there are often irregularities in form, as seen in Figure 5. From a general comparison of my osmic-acid preparations with those fixed in sublimate, I am inclined to believe that the nuclei often suffer distortion in sublimate, and that the spherical form represents a more faithful fixation. The excentric nuclei are never flattened nor invaginated, except in a few cases in which I have observed that one side of a nucleus was indented in such a way as to suggest mechanical distortion due to fixation. So fluid are the contents of the nuclei that it is not strange that such distortions should sometimes occur. These indentations, which are probably artificial, had no regularity in form or in position.

The nuclei must contain a very large proportion of fluid material which is not coagulated by the fixing agent. In both stained and unstained preparations the nuclei are much clearer than the surrounding cytoplasm. They contain a very small amount of matter that takes stain.

With very rare exceptions, there is but one nucleolus. It is always excentric, often very near the nuclear membrane, and generally departs little from the spherical form. In osmic-acid preparations the nucleolus is always sharply outlined and never exhibits anything but a perfectly homogeneous structure. It takes a quality of stain different from that of the chromatin, being somewhat brownish instead of dark blue or black. This is doubtless due to the fact that it does not take or hold the stain as strongly as the chromatin, the brown color being due to the osmic acid.

The chromatic substance is scattered about in the form of small granules, approximately spherical in shape but more or less irregular. They are often not sharply outlined and appear as if imbedded in some achromatic substance. The chromatic granules are mostly collected about the periphery of the nucleus where, with the achromatic substance, they form a very loose, irregular network. Many of the chromatic masses appear to lie directly upon the nuclear membrane. The central region of the nucleus is often quite free from chromatic material. The occurrence of small sharply stained chromatic granules close about the nucleolus, or lying directly upon its surface, is a very common condition. Figures 1, 2, and 3 show these well.

Rather coarse strands of achromatic material form more or less of a network between the chromatic masses. There is often a tendency toward a radial arrangement of this network about the nucleolus, which appears supported within the nucleus by that means (Figures 3 and 4). The nuclear membrane is always very sharply outlined, being emphasized at the median plane of focussing by the occurrence of chromatic masses upon it.

b. The Cytoplasm.

Very little can be said as to the finer structure of the cell protoplasm. The most careful examination fails to reveal its precise nature. It varies in degree of homogeneity somewhat according to the size of the cell. In the smaller cells (Figures 4, 7, 8, and 9) it usually appears compact and fairly homogeneous. In larger cells (Figures 2 and 3) it is much less homogeneous, and there is a tendency toward the formation of large vacuolar spaces, as seen at the process end of the cell in Figure 2.

The substance of the fixed cytoplasm, as it appears to the eye, may be said to be of four kinds. There is (1) a perfectly homogeneous "ground," represented by the lightest areas in the figures; (2) material which gives the impression of being very finely granular; in the smaller cells this material is quite evenly distributed, while in the larger cells it tends to concentrate in regions, giving the cytoplasm a blotchy appearance; (3) rather conspicuous granules or masses staining fairly deeply and often surrounded by an area within which the material of the second class is less dense, as best seen in Figures 2 and 3; (4) fine fibres irregularly distributed throughout the cell body, but often appearing to be associated with the more conspicuous granules and sometimes occurring about granules as centres of radiation, as can perhaps be recognized in some places in Figures 2 and 3. It is possible that the granules of the third class may be due simply to concentration of the finely granular material of the second class.

To what extent these appearances in the fixed cell correspond to structure in the living cell cannot be said. The occurrence of the larger granules or masses within clearer areas suggests coagulation effects, the substance of the clearer area having been massed at the centre of it by the action of the fixing fluid. It is quite likely, however, that there may be some structural basis for this effect. The occurrence of fibres radiating from these larger granules suggests that they may mark the more important centres of a cytoplasmic network.

In some cells, especially in certain ones of the brain, a system of fibres could be detected lying at the periphery of the cell and extending out into the nerve process.

In the larger cells no definite, sharply outlined cell membrane is ever seen. The cells appear to be enclosed by fine connective-tissue fibres, which form more or less of a capsule about them. Small nuclei, doubtless of non-nervous nature, often occur about the nerve cells, as seen in the regenerated cell of Figure 11 (Plate **2**).

c. The Centred System.

Evidences of concentric and radial structure are commonly seen, but the exact nature of this structure would be overlooked except in the most careful study, with the aid of oil immersion lenses.

Cells of the first type. — The conditions represented in Figure 1 may be considered typical for a large number of cells. This cell is from a section $6\frac{2}{3}\,\mu$ thick. In focussing up and down upon the section the eye is caught by a granule which is conspicuous by its size, sharpness of outline, and depth of stain. If it were a matter of a few cells or a single one, this might be a chance condition, but when a similar condition is commonly found in the observation of a large number of cells, we must conclude that we have not to do with an accidental granule. Moreover, when such a conspicuous body is found to occupy a definite and constant position in relation to other parts of the cell, and when it is found to be the centre of a system of radiating fibres, it is evident that the whole structure is one of importance. In speaking of the centre of this structure as a "conspicuous granule," it is not meant that it is the first thing that catches the eye in a casual glance at the cell. Many of the granules or masses, which have been described as forming the third class of constituents of the fixed cell, may be more prominent because of their greater size and their frequent occurrence within a clear area. But these larger masses differ from the central granule in being less deeply stained and less sharply outlined. The central granule is conspicuous as compared with any bodies in the finely granular cell substance. When once found, it is generally very easy to distinguish it from other elements contained in the cell body.

The position of the central granule is characteristic. It always lies in the part of the cell opposite the nerve process, and very nearly in the long axis of the cell. It is generally very near the nucleus, as in Figures 2 and 3; but it may be farther away, as in Figure 4, especially if much the greater bulk of the cytoplasm is on that side of the nucleus.

The central body of Figure 1 is a single minute granule, and is spherical, as nearly as could be determined for a thing so small. It lies at the centre of a very small spherical space which appears in the section as a narrow clear area about the granule. The clear area is not sharply outlined.

Several extremely delicate radiating fibres extend outward from the central granule into the surrounding cytoplasm. Those represented in the figure all lay in a plane parallel to the surface of the section. It was rarely possible to detect a fibre if it was so oblique that it did not come into the focal plane all at once. Generally not more than six or eight of these fibres could be detected. In all of the first nine figures can be seen fibres which extend well out toward the periphery of the cell. Many of the radiations, however, could not be traced so far. So fine are these radiations that it is only with the greatest difficulty that anything as to their nature can be made out. The more conspicuous radiations appeared to be made up of minute granules arranged in line. The finer radiations show no evidence of granules, appearing rather as most delicate hyaline threads. However, radiations were found exhibiting both characters at different parts of their course. It is therefore probable that these radiations consist of achromatic fibrils bearing more or fewer granules along their courses. The granules may be so thickly set that the radiation appears as a line of granules, or they may be absent, when only the achromatic fibril can be seen.

If a distinct radiation be carefully traced, it will be seen that at intervals there occur some fairly conspicuous granules, which are more easily seen because of a surrounding clear space. Figures 1, 2, and 3 show this to some extent, but the fact is much more clearly brought out in some of the regenerated cells to be described later (Plate 2, Figures 10–13).

Very often these granules, which occur along the course of a radiation, mark the point of divergence of secondary fibrils. In Figure 1, if the radiation which is most nearly in the axis of the cell be followed for one-third its length from the centre, a granule will be seen from which two fibrils proceed on toward the periphery of the cell. Figure 2 shows similar conditions, but the regenerated cells (Plate **2**, Figures 10–13) exhibit this arrangement more clearly.

Figure 2 represents a cell of the same type as that of Figure 1; but the central body is much nearer the nucleus, and is either elongated or else consists of two granules very close together. The central clear space is confluent with the clear spaces around two granules that lie in the courses of radiations from the central body.

Figures 5 and 6 are from acetic-sublimate preparations stained in iron-hæmatoxylin. They represent cells very similar to those just described. The attempt has been made to show something of the difference between the appearance of an osmic-acid and a sublimate preparation. The nuclear structures are fairly well brought out by the sublimate, but not so clearly as by the osmic acid. The structure of the cytoplasm is much less definite, but as far as it could be made out, it agrees with the description given for osmic preparations. Both cells show some evidence of an arrangement in the cytoplasm concentric about the centre of the radiating system. This is especially well marked in Figure 6.

Cells of the Second Type. — Figure 3 represents a cell in which a further complication of the radial system is introduced. The central body in this case appeared very large and of irregular form, but careful focussing resolved it into three granules of different sizes. They are surrounded, not by a clear space, but by a region which appears dense and very finely granular. The limit of this region is emphasized, in the section, by the occurrence of a number of stained granules which are arranged in the arc of a circle about the central granules. The radiations from the centre can be seen to include in their courses certain conspicuous granules lying in this arc. This finely granular region is evidently comparable to the "sphere" described by many authors. Figure 3 is strikingly similar to some of the figures in Bühler's paper of 1895.

Figures 7, 8, and 9 (Plate **2**) represent small cells of this type from the brain. In Figure 7 the body of the sphere differs in no visible way from the surrounding cytoplasm, but a number of granules form a complete circle about the central granule. In Figure 8 the entire radiating system is very faint, but there are evidences of two concentric circles. The structure in Figure 9 is very similar to that in Figure 3. The central body may consist of two granules, but they could not be clearly separated.

Figure 4 (Plate 1) represents a condition frequently met with. There is, in the cell drawn, a condensation of finely granular cytoplasm extending halfway from the centre to the periphery of the cell. This is probably in no way comparable to such a sphere as is shown in Figures 3 and 9. It is not sharply outlined, and it lacks the bounding layer of granules. The body at the centre of this finely granular region is surrounded by a clear space; and radiations, lacking, however, any conspicuous granules, extend toward the cell periphery. Cells of this character may best be considered as belonging to the first type (Figure 1), as far as the structure of the radiating system is concerned.

2. The Nerve Cells of Nereis.

In the ventral ganglia of Nereis are certain large cells situated near the median plane and having their nuclei in their dorsal or process ends. The nuclei are often flattened or invaginated on the side toward the cell centre. In one very large cell with an invaginated nucleus an intensely stained granule was seen lying in the concavity of the nucleus, and around the granule were several fine radiations. The cytoplasm was completely decolorized, the granule mentioned being the only stained object in it. This appeared to be a good case of the "centrosome." Nereis was not studied sufficiently to determine whether such structures are commonly present.

3. Outline of the Process of Regeneration of the Brain and Anterior Ganglia.

The regeneration of the anterior ends of the worms (Allolobophora) took place substantially in the manner described by Hescheler ('98). I have made no preparations at periods of regeneration earlier than seven days.

Figure 14 (Plate 3) represents a parasagittal section of the anterior end of a worm after seven days' regeneration. The limit of the old tissues is easily distinguishable in all such early stages, and, in fact, there is no difficulty, up to a comparatively late period, in distinguishing old tissues from those that are being regenerated. In Figure 14 the old epidermis ends at points designated by the asterisks. The new epidermis, between these points, is considerably thinner than the old. Underlying the new epidermis is a solid cicatricial mass of considerable thickness. The circular and longitudinal muscle layers are seen to end abruptly against the inner surface of the cicatricial mass. The anterior end of the alimentary canal is closed by the cicatrix and may remain closed for several weeks. The nerve cord also ends abruptly against the cicatricial mass. Even after the regenerating part of the cord is well established, the limit of the old cord is sharply indicated by the end of the old sheath, the inner homogeneous layer of which generally curls outward and backward a little at its cut end. In the preparation from which Figure 14 is taken, a more or less lens-shaped mass of newly formed cells lay near the end of the old cord. This is better seen in Figure 18 (Plate **4**), which shows the end of the cord drawn to a larger scale, — 160 diameters. Two mitotic cells (Figure 18, *cl. mit.*) are seen in the lens-shaped mass. The origin and nature of them will be discussed later (page 121).

Figure 15 represents a parasagittal section through the anterior end of a worm after sixteen days' regeneration. The regenerated parts are, as in the younger stage, included between two asterisks. The regenerated epidermis remains thinner than the old epidermis. A thin layer of circular (*mu. crc.*') and of longitudinal muscle fibres (*mu. lg.*') has been laid down in the conical regenerated end. The end of the old nerve cord is sharply marked by the extent of the sheath (*tu.*') and the abrupt termination of the mass of ganglion cells. Extending forward from the end of the old cord is a fibre tract, which runs out to the apex of the cone, lying ventral to the alimentary canal. The fibres become less distinct anteriorly, and are lost in a mass of cells underlying the epidermis. Along the ventral border of this fibre bundle is a thin layer of cells (*gn. nov.*) whence are to be derived the cells of the regenerated ganglia.

Figure 16 is from a parasagittal section of a worm after twenty-four days' regeneration. The regenerated parts are included between two asterisks. There is much variation as to the relative times of appearance of the regenerated organs. In Figure 15 (16 days) the regenerated muscle layers are well established. In Figure 16 (24 days) only a few longitudinal muscle fibres in the ventral part of the regenerated cone are to be seen.

In the sixteen-day preparation (Figure 15) the alimentary canal does not open to the exterior. In Figure 16 (24 days) the breaking through of the alimentary canal to the exterior is nearly, if not quite, accomplished. According to Hescheler the alimentary canal grows forward to meet a stomodæum or invagination of the epidermis, and the opening to the exterior is effected by a rupturing of the epithelial and epidermal layers, the epidermal invagination becoming the mouth cavity and the region posterior to the point of rupture becoming the pharynx. In the preparation from which Figure 16 is taken, the epidermal invagination has progressed to meet the alimentary epithelium. In some sections a delicate layer of the epithelium was found still closing the end of the canal (see Figure 16). In other sections this layer was broken away, probably accidentally.

As to the nervous system, Figure 16 represents a much more advanced stage of regeneration than Figure 15. In this advanced stage the end of the old cord is as sharply marked as ever. The new fibre tract has extended forward to encircle the alimentary canal, the two branches uniting in a small mass of cells (*gn. su'oes.*) above the stomodeal invagination. This mass of cells constitutes a well-defined brain fundament.

After the condition of Figure 16 has been reached, we have to do only with growth and segmentation of the parts already laid down. I made no preparations of material regenerated more than forty days. There is much individual variation as to the rapidity of the process. In one animal after thirty-four days' regeneration the brain was scarcely smaller than in the normal worm and had come to occupy its position in the third segment. The number of segments regenerated in this case could not be determined. The brain and anterior end of the ventral cord in this animal could hardly be distinguished from those of a normal worm except for the occurrence of numerous dividing cells at the anterior tip of the cord and in the posterior dorsal region of the brain. The sheaths enclosing the new nervous parts were well developed. But in most of the worms, after thirty-five to forty days' regeneration, the regeneration of the nervous parts had not reached so advanced a stage.

The foregoing statements are sufficient to give a general outline of the process of regeneration. Hescheler ('98) has described the process in more detail; as far as my observations go, my results agree with his. I now propose to discuss the origin of the new nervous parts more minutely.

4. Origin of the Cells of the Nervous Fundaments.

According to Hescheler the cells which give rise to the regenerated brain and ventral ganglia are derived chiefly from the epidermis. The cicatrix is at first composed of lymph cells and spindle-shaped cells of doubtful origin. Later appear cells with nuclei like those of the epidermis. These he believes to be derived chiefly from the epidermis, but some may come from the alimentary epithelium and some from certain large nuclei found in the muscle layers. In addition to these sources there is mitosis within the old nerve cord which doubtless gives rise to cells that assist in the regeneration.

From my own preparations similar conclusions as to the origin of the regenerated nervous elements must be drawn, except that only in rare cases is there any evidence that cells of the old cord assist in the regeneration.

In the preparation from which Figure 14 is taken, the cicatrix (*cic.*) is a solid mass composed mainly of greatly elongated spindle-shaped cells with small oval or elongated nuclei. Figure 17 represents a number of these cells more highly magnified. The nuclei are totally unlike epidermal nuclei, being much smaller, of different shape, and lacking a prominent nucleolus. Epidermal nuclei drawn to the same scale as Figure 17 may be seen in Figures 43–45 (Plate 6). There are also present in the cicatricial mass some very small spherical nuclei. These are doubtless nuclei of lymph cells, for they present exactly the appearance of the nuclei of the lymph cells commonly found in the body cavity. These lymph cells, in some preparations, are much more numerous in the regenerating region than elsewhere, often occurring in almost solid masses.

There is individual variation as to the character of the cicatrix. In most of my preparations of early stages (7 to 11 days) the cicatrix was composed chiefly of the spindle-shaped cells. In one eleven-day preparation, however, there was only a small mass of cells underlying the regenerated epidermis, and this mass was composed mainly of cells with large nuclei having all the characters of epidermal nuclei. These cells were actively dividing. Figure 57 (Plate 8) shows a group of these nuclei.

According to Hescheler the spindle cells give rise to the new muscle layers. In my preparations of later stages, too, these spindle cells are seen to be taking the direction of the fibres of the two muscle layers in such a way as to leave no doubt as to their fate. After the first week or two the spindle cells form a smaller proportion of the cicatricial mass at the regenerated end, this fact generally being due to the accumulation of these cells into the new muscle layers. The remaining scattered elements are either lymph cells or cells with large nuclei of the epidermal type. The latter cells tend to collect in the region into which the regenerating cord is extending.

The forward growth of the fibre bundle precedes the accumulation of cells about it ventrally and laterally in the position of the ganglionic masses.

Of the three kinds of nuclei to be met with among the incompletely differentiated cells of the regenerating region, there is no evidence that either the lymph nuclei or the nuclei of the spindle cells give rise to new nervous elements. The nuclei of these two types are totally unlike the nuclei which are first found associated with the new nervous parts, and there is no evidence of a transformation of one kind into the other. Granting this, the origin of the new nervous elements must be referred to the larger nuclei, those of the epidermal type. That these large nuclei are derived from the epidermis, there is good evidence in the preparations.

The formation of a new epidermis over the cicatrix offers some interesting problems, which, however, require a study of earlier stages of regeneration than any I have worked with. After seven days there is always found over the cut end of the worm a continuous thin layer of more or less flattened epidermal cells, and a thin layer of cuticula also is already formed. In rare cases I have found mitosis in the epidermis at this early stage. At later stages there is abundant mitosis in the new epidermis, and in one case numerous dividing cells were found among the basal or subepidermal cells back through several uninjured segments. Some signs of *amitosis* were found in the regenerated epidermis, but not conclusive evidence. Nuclei were found with two nucleoli, and several columnar epidermal cells were found containing two nuclei pressed so closely together that their contiguous surfaces were quite flat, suggesting that there had been a direct division and that the two nuclei had not yet moved apart. In one case four nuclei in a common cytoplasmic mass were found so closely pressed together that the group presented the appearance of the four-cell cleavage stage of an egg. No nuclei in process of constriction were observed.

The new epidermis having once been established, there is little room for doubt that its later increase is effected by the mitotic division of its own cells. It is after the first week that we find evidence that not all the cells produced by the epidermis are destined to remain epidermal cells.

The normal epidermis consists of a single layer of columnar cells with some basal cells of irregular form wedged in among their deep ends. The nuclei of these basal cells are unlike those of the columnar cells. They are smaller, often lack a prominent nucleolus, and generally present a darker appearance, due to a greater proportion of chromatic material. In the regenerated epidermis places are often found where certain cells, with nuclei of the kind characteristic of the columnar cells, tend to form a second layer. Single cells are found so placed as to suggest that they are being pushed down below the surface layer. Others, apparently, have been quite displaced from their superficial position and lie free underneath the epidermis. There may frequently be found small masses of cells with nuclei precisely like those of the epidermis, lying close to the deep surface of the epidermis, and so far removed from any other tissue containing similar nuclei that their epidermal origin is beyond doubt.

The surface of the regenerated end is often very uneven in the early stages. The new epidermis is thrown into folds or marked by elevations and pits. At an inner angle of a sharply invaginated region of epidermis may sometimes be seen evidences of an inward proliferation of the epidermal cells. There is also some evidence, as Hescheler finds, that not only single cells, but also considerable masses of cells, may be pushed in and separated from the surface layer. Small local invaginations are sometimes found which are nearly closed over, and in one or two places I have seen small cavities completely enclosed by epidermal cells, as if small invaginations had become closed over and had sunk beneath the surface.

In one animal of twenty-four days' regeneration the new nerve cord was already well established. The region of the epidermis nearest the anterior end of the regenerating cord consisted of loosely aggregated cells. Between this region and the end of the cord were numerous scattered cells with nuclei like those of the epidermis and also like those of the cells already definitely associated with the new cord. The scant cytoplasm of these scattered cells was more or less drawn out to spindle shape, and most of the cells were placed with their long axes extending in the direction of the nerve cord. Similar conditions were found in other animals. The appearance indicates a separation of cells from the epidermis and the migration of these cells in toward the regenerating cord.

All the facts taken together justify the belief, as Hescheler concludes, that the epidermis is an important source of cells that take part in regeneration, and especially of cells that go to the regenerating cord.

There are other possible sources of the nuclei which resemble those found in the regenerating cord. The alimentary epithelium contains such nuclei, and it is not impossible that it may furnish cells for the regeneration of other organs, but there is no good evidence for believing that it does so to an important extent in the case of the nervous system. There are scattered nuclei among the muscle fibres, and elsewhere, which resemble the epidermal nuclei, and these may also take part in regeneration.

Three facts justify the conclusion that the cells of the new brain and ganglia are mainly of epidermal origin. (1) In the early stages of regeneration the nerve cord is in more intimate relation with the epidermis than with any other tissue. (2) The new nervous parts are laid down in a region whose cells (with the exception of the lymph cells and the spindle cells) are doubtless derived mainly from the epidermis. (3) There is an apparent inward shifting of cells from the epidermis to the new cord.

One possibility remains to be considered. Hescheler finds, in regenerating worms, abundant mitosis in the ganglia of the old cord back through some fifteen segments, and concludes that the old cord furnishes some material toward regeneration. This increase of cells in the old cord has not been commonly found in my preparations. In most of the series that have been carefully studied there was no evidence whatever of mitosis or increase of cells in the old cord. In one or two animals a condition was found similar to that described by Hescheler. In one worm of ten days' regeneration were found several masses of cells presenting an appearance unlike anything to be found in a normal ganglion and containing so many mitotic cells as to indicate a rapid increase. The preparation included nine segments back of the injured segment. The most posterior mass of proliferating cells was in the eighth segment. Several similar masses occurred in ganglia of more anterior segments and occasionally isolated dividing cells were found.

In the worm from which Figure 14 (Plate **3**) is taken, the mass of cells which has already been mentioned (page 116) as lying at the anterior end of the old cord is doubtless of the same nature as those found farther back in the other animal. This preparation included only five segments and no similar masses were found in other segments. In appearance the cells of this mass (Plate **4**, Figure 18) are precisely like those of the more posterior groups of the other worm, and unlike any found in the near-by cicatrix. These facts, and the position of the mass well within the limit of the old cord, make it scarcely to be doubted that the mass owes its origin to the increase of cells of the old cord, rather than to any cells which may have wandered in from the cicatrix.

It is the occurrence of masses of actively dividing cells, rather than the character of the individual cells or nuclei, that distinguishes this from the condition found in the cord of a normal worm. The nuclei of these cells differ in no marked way from nuclei which may be found in the ganglia of uninjured worms. They are smaller than the nuclei of the large nerve cells, but they show the same structure as to chromatic material and the presence of a single large nucleolus. Figure 57 (Plate 8) shows some cicatricial cells of the epidermal type, but the same drawing would represent equally faithfully a group of cells from one of these masses in the old cord. The nuclei differ from any found in the normal cord mainly in being more or less elongated. In Figure 18 it can be seen that the nuclei in the thin posterior end of the mass are more elongated than those in the thicker anterior part of it. This condition suggests a mechanical deformation of the nuclei as a result of the rapidly growing mass pushing its way back into the tissue of the cord. There was scant cytoplasm about these nuclei and no definite cell outlines, as is also the case in the nuclei of Figure 57.

The absence of this cell increase in the old cord of many animals shows that it is not a necessary feature of the regenerative process. The presence of one of these masses of cells exactly at the region of injury, as in Figure 18, makes it probable that it provides material for regeneration. It can hardly be supposed that an increase of cells in ganglia situated five or ten segments back of the region of injury has anything to do with the actual regeneration of new ganglia anterior to the old cord.

5. Histology of the Nervous Fundaments.

Having considered the origin of the cells which constitute the fundaments of the brain and new ganglia, I now propose to consider certain questions pertaining to the development of the nerve cells from the cells of these fundaments. The main purpose at this point is to determine if any polar structures of a mitotic cell pass into the resting cell, persisting through all the stages of growth and differentiation to become, or give rise to, the centred system of the mature nerve cell. It is therefore necessary to examine the mitosis, and especially the later stages of it, in the cells of the fundaments, and to find, if possible, a series of cells which shall represent successive stages in the development of nerve cells.

Preparations from the later stages of regeneration were found most favorable for this purpose. In worms of from thirty to forty days' regeneration the new brain and ganglia were represented by large masses of cells, among which dividing cells were very abundant. In the same animals the differentiation of nerve cells was in progress, and frequently a single section contained not only dividing cells with scant cytoplasm, but also large, apparently fully developed nerve cells, and perhaps many intervening stages.

In the earlier stages of regeneration, cells in a solid mass, showing no signs of segmentation, are found lying laterally and ventrally about the fibre bundle which has previously marked out the position of the nerve cord. In the brain fundament a similar mass of cells lies about the neuropile, chiefly on its dorsal and posterior border, as seen in Figure 16 (Plate **3**). This position of the cells is characteristic. These cells have a very small amount of cytoplasm, so that the fundaments look like masses of solidly packed nuclei. There are no distinct cell outlines, but where the nuclei are less solidly aggregated an irregular mass of cytoplasm may be found collected about each one. At sufficiently early stages the nuclei are all alike, ellipsoidal or spherical in form, and generally have a single large spherical nucleolus. Nuclei without a nucleolus are often found. They may belong to cells which have recently divided. The absence of the nucleolus is often associated with a condition of the chromatin which indicates a recent or approaching division of the nucleus.

At later stages of regeneration many of the nuclei lying deeper in the mass become larger and more nearly spherical and accumulate a considerable body of cytoplasm about them. *Cells which assume this character have ceased dividing and are in process of development into nerve cells.* The nuclei on the outer borders of the fundaments retain their embryonic character and continue actively dividing.

The more advanced the stage of regeneration, the more nearly have the deeper cells attained the character of typical nerve cells.

Figure 20 (Plate **4**) represents a parasagittal section through the brain of a worm after thirty-four days' regeneration. The regenerated brain is smaller than the normal brain. (Compare Figure 20 with Figure 19, a similar section from the corresponding region of the brain of a normal animal.) The cells occupy the posterior and dorsal border of the neuropile. This relation of cells and fibre mass is found at the earliest stages in the fundament (Figure 16) and persists through all the later development. It is characteristic also of the normal brain. (Compare Figure 19.) In the deeper part of the cell mass (Figure 20) may be seen a number of pear-shaped cells with their processes directed toward the centre of the neuropile. These cells are, to all appearance, fully differentiated nerve cells, like those occupying similar positions in the normal brain. Between these cells and the periphery are smaller cells, some of them pear-shaped and with processes, others in which no processes could be found. About the extreme posterior border is a mass of nuclei with indefinitely assignable cytoplasm and exhibiting abundant mitoses, — exactly the condition which the entire cell mass of the fundament presents at earlier stages.

It is evident, then, that the deeper cells are the first to become differentiated into nerve cells, while the cells on the periphery of the mass long retain their embryonic character and continue dividing to give rise to new elements.

In the normal brain (Figure 19) the large typical nerve cells occupy a deep position. About the posterior border of the brain are smaller cells, some pear-shaped and with processes, others apparently lacking processes. There are also nuclei like those of the smaller pear-shaped cells, but having very scant cytoplasm, or there may be several of them lying near together in what is, to all appearance, a common cytoplasmic mass. Such nuclei, or groups of nuclei, differ in no visible way from the actively dividing nuclei which constitute the early fundaments. They resemble likewise the peripheral layer of nuclei present at so late a stage of regeneration as is seen in Figure 20. If it could be assumed that the embryonic development of the normal brain is similar to the regenerative development, there would be little reason for doubting that the small cells and "indifferent" nuclei of the posterior border of the normal brain represent the mass of embryonic cells which have given rise to the differentiated nerve cells. There is little or no reason for regarding them as neuroglia cells. The nuclei which, beyond question, belong to the neuroglia are of an entirely different character.

Conditions in the regenerating cord are similar to those in the brain. The deeper cells are first differentiated into nerve cells, while the cells along the ventral border and at the anterior tip of the ganglionic mass continue dividing long after the deeper cells have attained the size and form of typical nerve cells.

6. Mitosis in the Nervous Fundaments.

Figures 21 to 30 are taken from the actively dividing cell masses in the regenerating brain and cord of animals after about five weeks' regeneration. As already mentioned, these cells have very little cytoplasm and there are no definite cell outlines. Often the nuclei are packed so closely together as to appear imbedded in a common cytoplasmic mass. In the resting cells of this character I have been unable to discover any structure which could, beyond doubt, be taken for a centrosome. If present, it must be an extremely minute body, and all the conditions are most unfavorable for its discovery. It is not until the cell has passed into the earlier stages of mitosis that an unquestionable centrosome is to be observed.

Cells in the early prophase are numerous and generally present the appearance of the cell at the right in Figure 21. Such cells are conspicuous objects because of their sharply defined spherical outlines and the clear area surrounding the chromatic elements. The sharp outline is due to the presence of a distinct membrane, and, for reasons to be given later, this membrane must be considered to be a cell membrane and not an expanded nuclear membrane. At some time during the formation of the chromosomes the nuclear membrane disappears.

The appearance of the cells at this stage indicates a condition of turgescence. The entire cell contents, cytoplasmic as well as nuclear, with the exception of the chromatin, are in a highly fluid condition, judging by the absence of stained substance (except the chromatin) in the preparations. That there is a swelling of the cell during the beginning of mitosis is proved by such conditions as are seen in Figure 21. Here are two dividing cells close together. The one at the right is in the prophase, while the one at the left is in the metaphase. (The axis of the spindle in the latter cell is oblique to the plane of the section, and one pole has been cut away. The remainder of the cell was easily identified in the next section.) The two mitotic cells have increased in volume; and the large nucleus of another cell, caught between them, has been pressed out of shape by the combined pressures from the two swelling cells.

The smallness of these cells and the large number of chromatic elements make it difficult to determine the exact manner of formation of the chromosomes. One or two nuclei have been found which gave some evidence of a spireme condition of the chromatin, but, aside from these, the earliest condition of the chromosomes was that seen in Figure 21, where the chromatin is in the form of large, nearly spherical granules. The number of chromosomes could not be accurately determined.

The presence of a centrosome was not observed until the spindle had been well formed. The two granules lying at the edge of the chromatic mass in Figure 21 (cell at the right) may be the centrosomes which have not yet taken their position at opposite poles. Cells were found where the two poles of the spindle had been established, and the chromosomes were not yet aggregated into an equatorial plate. Sometimes an extremely minute centrosome could be distinguished at the poles of the spindle at this stage. When the cell is in the metaphase the centrosomes are generally conspicuous objects, although there is much variation as to their size. The half spindle in Figure 21 (cell at the left) shows a centrosome. In Figure 22 the centrosomes are unusually large for cells at that stage. The average size of the centrosomes is perhaps fairly indicated by Figure 24.

In the metaphase the cell membrane is still present. The loss of a perfectly spherical form may mean a decreased internal pressure. Particular attention is directed to the fact that there is very little stained material outside the limits of the spindle. Figure 23 represents a very typical metaphase. Except for a slight cloudiness near the poles, the cell body is quite clear. The spindle is very sharply outlined, and at its poles are minute deeply stained centrosomes. No polar radiations are visible. In Figure 22, except for a few indefinite irregular masses of unstained material, the body of the cell is clear. In this case, however, a few very indefinite polar rays could be seen. In Figure 24 there is an unusually large amount of material, apparently finely granular, in the region of the two poles, and into this material extend some well defined polar radiations. The half spindle of Figure 21 shows an extreme case of the presence of solid substance outside the spindle.

In the metaphase, then, the body of the cell is generally clear. If solid material be present outside the limits of the spindle, it tends to be accumulated about the poles and may be associated with polar radiations.

The division of the chromosomes must take place at a very early stage of the equatorial plate, for in most of the cells in the metaphase the chromosomes are in a double layer.

The region occupied by the spindle always presents a compact and homogeneous appearance, although not deeply stained. A limited number of conspicuous fibres may be seen lying upon the surface of the spindle. These are quite likely "mantle fibres" attached to the chromosomes. They exhibited a finely granular structure.

The anaphase must be a period of very short duration, for figures in which the chromosomes were just separating, or had traversed less than half the distance toward the poles, were rarely found. The few that were found exhibited no unusual features.

Figure 25 represents a cell in which the chromosomes have nearly completed their migration toward the poles. At the right pole the chromosomes are aggregated into a nearly solid mass. At the left pole they are still somewhat scattered. The sharp cell outline is still preserved, indicating the presence of the cell membrane. There is a very slight equatorial constriction of the cell. The body of the cell, outside the spindle figure, is perfectly clear except for a slight trace of indefinite material on one side of the spindle. The interzonal filaments occupy a barrel-shaped region. This shape of the figure is characteristic for this phase, and cells in this condition were very abundant. The barrel-shaped figure lies sharply outlined in the surrounding clear space. The interzonal filaments are of granular appearance, and some irregular dark masses occur upon them.

The presence of a centrosome at the left pole of the figure is doubtful. The black granule which appears to occupy the position of the centrosome is much larger than the centrosome usually is at this stage. It is possibly an aberrant chromosome. The axis of the figure is oblique to the plane of the section, the left end being higher. This position favors the obscuring of a centrosome. Although the chromosomes at the right pole are in a nearly compact mass, something of the form of individual chromosomes is still to be distinguished. The centrosome is unmistakable, lying at the apex of the old spindle. The chromatic mass is more smoothly outlined on the polar side, being concave toward the centrosome. This condition is characteristic and is seen to better advantage in the cell represented in the next figure.

Figure 26 is a somewhat later stage than Figure 25, as is shown by the complete consolidation of the chromosomes and the deeper equatorial constriction of the cell. The cell membrane is still distinctly present, although at some regions it appears fainter and less clearly defined. The cell body, outside the region of the spindle, is still nearly clear. The figure itself is barrel-shaped, as before, but the interzonal filaments are more sharply bent at the equator. Each group of daughter chromosomes appears to have fused to a solid mass. In the mass at the right pole the position of a lagging chromosome is indicated by a chromatic process extending toward the equator.

The important feature at this stage, in its relation to later stages, is the condition on the polar side of the chromatic mass. Each chromatic mass is concave on the side toward the centrosome and convex on the opposite side. The polar and equatorial surfaces of the chromatin lie in the surfaces of two spheres whose common centre is marked by the centrosome. These conditions point to the centrosome as the centre of the forces by which the chromosomes have been moved toward and grouped around the poles.

Between the centrosome and the polar surface of the chromatin is a region otherwise bounded by a conical surface extending from the centrosome, as apex, to the nearer outer edge of the chromatic mass. This is the region originally occupied by the end of the spindle, but at this stage it is impossible to detect any fibres extending from the centrosome toward the chromatin. This polar region is stained sufficiently to be sharply outlined against the outer clear space of the cell, and yet it is so much lighter than the chromatin as to be clearly distinguished from the chromatic mass. It appears perfectly homogeneous, exhibiting neither fibres nor granules.

This condition of chromatin and polar structures persists for some time while certain equatorial changes occur. These changes include the formation of a membrane between the daughter cells (Plate **5**, Figure 27). The figure meanwhile loses its barrel shape, assuming the form of two cones with apices together at the plane of the new membrane. The axis of the entire figure may become bent at the meeting of the two cones. The axis of the left daughter cell in Figure 27 is almost parallel to the plane of the section. The chromatic mass is of characteristic appearance, but the centrosome was not clearly to be made out. The axis of the right daughter cell extends obliquely upward, so that the centrosome is obscured, and the observer looks down into the concavity of the chromatic mass. The interzonal filaments are not sharply constricted at the equator. The fact that varying degrees of equatorial constriction of these filaments may be found, supports the view that the fibres are carried inward toward the axis of the figure by an ingrowing membrane. However, in most cells at this stage may be found traces of fibres still occupying the region formerly filled by the barrel-shaped figure. Such fibres are to be seen in Figures 27–29.

Two facts of importance are to be noted at the stage of Figure 27. The original cell membrane is in process of degeneration, the clear space about the mitotic figure being no longer sharply outlined. It is of irregular form, as if being encroached upon by the cytoplasm of near-by cells. The second fact is the presence of considerable loosely aggregated, rather granular material outside the limits of the constricted figure. As the volume of the constricted figure is much less than that of the barrel-shaped figure which precedes it, and as the material in question is mainly in the region formerly occupied by the barrel-shaped figure, it is reasonable to conclude that this material is some of that originally contained within the limits of the larger figure.

In Figure 28 one chromatic mass has been cut away. The centrosome of the other pole is not visible, probably because of the obliquity of the axis. Something of the lightly stained polar region can be seen. The old cell membrane has degenerated to a less extent than in Figure 27. A distinct equatorial membrane is present, and the interzonal filaments are sharply constricted. Outside the constricted figure is some loose material, as in Figure 27, and a few fibres from the chromatic mass mark the outlines of the former barrel-shaped figure.

Figure 29 is a reconstruction. The left chromatic mass was cut away from the rest of the figure, being found in an adjacent section. The old cell membrane is indistinct. The equatorial membrane is clearly present. The interzonal filaments are sharply constricted, and there is a suggestion of a "Zwischenkörper." There are some traces of fibres outside the constricted figure, but, except for these, *the space outside the figure is almost clear.* The chromatin appears enclosed in a membrane, and the daughter chromatic masses show considerable increase in size. The chromatin is in the form of large granules. At the polar side of the left chromatic mass (nucleus?), the lightly stained region and the centrosome are to be seen. These could not be seen in the other daughter cell, perhaps because of the position of the axis. The condition of the chromatin in this case is much more advanced than ordinarily when the interzonal fibres are still present.

In Figure 30 the chromatic masses are in much the same condition as in Figure 27. Owing to the obliquity of the axis of the right daughter cell, the centrosome is not to be seen. The old cell membrane is fairly distinct in some regions, but quite lacking in others. The interzonal filaments are sharply constricted. There is, again, a suggestion of a Zwischenkörper, although the concentration of the fibres may account for the darkness at their equatorial region. The important points to be noticed are, first, that the daughter-cell bodies outside the limits of the constricted figure are practically clear, and, secondly, that there is no trace of an equatorial membrane. The constriction of the old cell outlines and the constriction of the interzonal filaments would indicate that the equatorial membrane had been formed and has disappeared.

7. Development of the Nerve Cells.

The significance of these facts concerning the cell membranes will best be understood after a description of Figures 31–36 (Plate **5**), which represent further stages in the progress of recently divided cells toward a resting condition. That such objects as are seen in these figures are what I have taken them to be admits, I believe, of no doubt. They occur with about the same frequency as the later stages of mitosis. Moreover, there are no other objects present which could possibly be taken for recently divided cells. They are found in pairs oftener than would occur by chance. That they seem not always to occur in pairs may be explained, in part, at least, by two facts. It is frequently observed that two sister nuclei may progress toward the resting condition with very unequal degrees of rapidity. There is much evidence that this is so in the case of these cells. Figures 32 *a* and 32 *b* represent two objects which lay so close together as to leave no doubt as to their being sister cells, but there is a marked difference in the size and compactness of the chromatic masses. It must be that one of two sister cells may so far outstrip the other in regaining the resting condition as to leave the slower cell apparently without a mate. Secondly, when two sister cells lie in different sections, having found one, it is difficult to identify the other, especially if they are not alike in appearance.

It often happens that two very similar young nuclei are found, not so very far apart, but yet farther apart than they could have been at the end of mitosis. In some regions of the fundaments of the nervous parts the cells are very loosely aggregated, the spaces doubtless being filled with fluid in the living animal. It seems probable that there may be a mechanical shifting of the less securely supported cells, merely as a result of the muscular activities of the animal. In this way young sister cells may become separated from each other.

Figure 31 represents a young cell from the ventral posterior border of the regenerating brain, together with three nuclei of adjacent resting cells. A similar object was found in the next section, but at a distance considerably greater than could have intervened between the two at the end of a mitosis. If the darkly stained object in Figure 31 be compared with the chromatic masses and their accompanying polar structures in Figures 26–30, it will readily be seen that the disappearance in the latter of that part of the spindle which lies between the two chromatic masses, and the assuming of a more nearly spherical form by the chromatic masses would result in two objects like the one seen in Figure 31. Figures 32 *a* and 32 *b* represent two young sister cells with several of the surrounding nuclei. They lay in two adjacent sections, and by means of camera drawings their centres were found to be exactly superposable.

The interpretation of Figure 31 is obvious. The heavily stained compact mass, concave upon one side, otherwise spherical, is one of two daughter chromatic masses resulting from the fusion of a group of daughter chromosomes. On the concave side of the chromatin is an area distinguished by a stain distinctly lighter than that of the chromatin, but yet sufficiently heavy to outline it sharply against the outer clear space. On the mid-border of this lightly stained region is a dark granule. This granule is the centrosome, and the lightly stained region corresponds to the polar region of the old spindle. The chromatic mass and its accompanying polar structures lie in an irregular, indefinitely outlined, clear space. This clear space is the region formerly limited by the old cell membrane, which has completely disappeared. In the later stages of mitosis represented in Figures 27–30 various stages in the degeneration of the cell membrane of the mother-cell are to be seen. The dark masses (Figure 31) lying in the clear space, on the apolar side of the chromatic mass, may be remnants of the old spindle.

In Figure 32 *a* is a similar condition of the chromatic mass with the lightly stained polar region on its concave side. No distinct centrosome was visible in this case. The surrounding clear space marks the region formerly bounded by the daughter-cell membrane. In Figure 32 *b* a more advanced condition of the chromatin is seen. The volume of the chromatic mass has increased, and this increase is attended by the separation of the chromatin into a number of large granules, between which the mass has a lighter appearance. The concavity on the polar side of the chromatin is still marked. The lightly stained polar region is sharply outlined. It has increased in volume and lost its conical form. The centrosome no longer lies at its border, but well in toward the concavity of the chromatic mass. There are some faint lines extending from the centrosome to the periphery of the lightly stained region. Chromatic mass and polar structure lie in a clear space.

Figure 33 shows two pairs of sister cells. α and β are to be regarded as the chromatic masses of one pair. The chromatic masses of the other pair lie one over the other. γ is the upper of the two masses, and the outline of the lower is indicated by δ. In α and β the condition of the chromatin is much as in Figure 32 *b*. α shows the concavity of the chromatic mass, the lightly stained polar region, and the centrosome at its apex. β is in an unfavorable position for the observation of the polar structures. α and β lie in a common clear space, which shows a constriction in the region between the two chromatic masses. This common clear space is that formerly bounded by the mother-cell membrane. The equatorial membrane, separating the two daughter cells, has disappeared. γ and δ are unfavorably situated for study.

Figures 34 and 35 represent two young cells whose sister cells could not be identified. The chromatic masses are in the same condition, both showing the polar concavity and the loosening of the chromatin into large indistinctly separable granules. In both cases the lightly stained polar region and its centrosome are present, and in both cases a thin layer of lightly stained material extends from the polar region along one side of the chromatic mass to its opposite end. In Figure 35 a slightly clearer area bounded by a darker ring surrounds the centrosome. In both figures a clear space surrounds the ellipsoidal body, which is composed of the chromatic mass plus its polar structures.

Figure 36 shows a group of cells from the posterior ventral border of a regenerating brain. At the centre of the group is a young cell. The chromatic mass is composed of indistinctly separated granules. On one side of it is the lightly stained polar region within which lies a dark granule, doubtless the centrosome. On the border of the lightly stained region are two dark places, but focussing shows that they are not distinct granules. There is no marked polar concavity of the chromatic mass. The surrounding clear space belonging to the daughter cell is well defined.

Above the dividing cell in Figure 29 is a young cell which shows the swelling chromatic mass, the polar region, centrosome, and the clear space about the entire stained object.

Figures 37 and (Plate **6**) 38 show later stages in the condition of the chromatic masses; it is not until such stages as these are reached that answers can be confidently given to the questions, which already must have suggested themselves. How much is nucleus and where is the cytoplasm in Figures 31–36? Unless one is prejudiced by holding the belief that the centrosome must lie outside the nucleus, there are two possible interpretations of the object shown in Figure 32 *b*. It may be that the nucleus is identical with the chromatic mass, or it may be that the new nuclear membrane is represented by the elliptical outline which encloses the chromatic mass together with the lighter region at its pole. Upon careless observation with a dry objective, one would hardly hesitate in saying that the elliptical outline is that of the nuclear membrane.

According to this interpretation, the centrosome would lie within the nuclear membrane.

When the condition of Figures 37 and 38 is reached, it becomes evident that *the lightly stained polar region is not included within the nuclear membrane.*

Figure 38 shows a group of cells from the anterior end of a regenerating cord. At the centre of the group is a large nucleus slightly irregular in form. It contains a single nucleolus and is denser in chromatin than most resting nuclei. On one side of the nucleus is a lightly stained region, appearing crescent-shaped in the section, and sharply outlined against the clear space which surrounds it and the nucleus. At the mid-periphery of the light region is a dark granule. A comparison of Figure 38 with Figures 31–36 leads to the conclusion that *the chromatic masses of Figures* 31–36 *are the daughter nuclei, and the lightly stained polar regions including the centrosome are not contained within the nuclear membrane, but represent cytoplasmic structures.*

Figure 37 shows a cell from a regenerating brain. The nucleus, containing a large proportion of chromatin, still exhibits the polar concavity seen in the earlier "chromatic masses." No nucleolus is yet visible. In this case the lightly stained region on the concave side of the nucleus is of much greater volume in proportion to the nucleus than in Figure 38. Near the mid-border of it is a small deeply stained granule surrounded by a slightly clearer space. Some weak radiations proceed from the granule. In Figure 37, then, we have a nucleus, upon the concave or polar side of which is a considerable mass of cytoplasm containing a centrosome and radiations. But what of the clear space surrounding the nucleus and its polar mass of stained cytoplasm? In all the stages represented in Figures 31–38, this clear space is present. It can be interpreted only as the space originally bounded by the mother-cell membrane, which has now degenerated. In such a case as Figure 37, is the clear space to be regarded as a part of the cell territory belonging to the nucleus which lies within it, or is the entire daughter cell at this stage to be considered as included within the outline which encloses the nucleus and the dense cytoplasmic mass lying on its concave side? I hold the latter to be the correct interpretation. In all of Figures 31–38, *the lightly stained polar region containing the centrosome constitutes the fundament of the cytoplasm.* This cytoplasmic fundament increases in volume along with the nucleus, occupying more and more of the space originally bounded by the old cell membrane.

At all stages it must be said that all the *living parts,* at least, of the daughter cell are included within the limits of the nucleus and its polar cytoplasmic fundament. It may be that the surrounding clear space contains fluid material derived from the degenerated parts of the mother cell, and that the growing cytoplasm of the daughter cell utilizes some of this material. In that sense only can the clear space be regarded as actually a part of the young cell.

Figure 39 shows two cells from a regenerating subœsophageal ganglion. The nucleus at the left is in a typical resting condition, having a chromatic network and large nucleolus. Its cytoplasm is massed at one end of it and contains the centrosome surrounded by a dark ring. The nucleus at the right shows no nucleolus. The cytoplasm is massed at one end of the nucleus and contains a clear space at the centre of which is a dark granule with some weak radiations. The young cells of Figures 34 and 35 may readily be imagined to become such cells as are seen in Figure 39.

Figures 40 and 41 represent cells from the brain after five weeks' regeneration. The nuclei have the form and structure typical for those of nerve cells. The cytoplasm in both cases is collected upon one side of the nucleus and contains an unmistakable centrosome and radiations, constituting a centred system like that which has been described in nerve cells of the normal worm. No nerve processes from these cells could be seen. Cells like these may be derived from cells like those in Figures 37 and 39 simply by the increase in volume of nucleus and cytoplasm. By this growth the space originally bounded by the old cell membrane becomes entirely filled, and there is no longer a clear space about the growing cell.

In Figure 36 the large nucleus at the extreme left possesses a considerable cytoplasmic mass, which contains evidence of a centred system, although no distinct centrosome could be seen. The nucleus is peculiar in lacking a nucleolus. The cell at the extreme right has a pear-shaped form, and there is some evidence of a process at the smaller end. On the side of the nucleus toward the larger end of the cell is a region of denser cytoplasm with a lighter centre, but no centrosome or radiations can be seen.

Figure 42 shows a group of three cells from a subœsophageal ganglion of thirty-four days' regeneration. The three nuclei lie at different levels, the smallest one being lowest. A centrosome and radiations may be seen close to each of the two larger nuclei, and on the side toward the greatest cytoplasmic mass.

8. The Centrosome in the Mature Regenerated Nerve Cells.

Evidences of the presence of the centred system are to be found in cells of all sizes from those represented in Figures 40–42 (Plate **6**) to the fully differentiated nerve cells such as are shown in Figures 10–13 (Plate **2**), which are from a brain of thirty-four days' regeneration. The cells shown in Figures 10–12 lay side by side in a single section of the brain. Figure 10 represents a cell whose centred system places it among cells of the "first type," as described (pages 112–114) for cells of the normal animal. The whole structure in this case was unusually distinct. The centrosome (for so it can now be called) lies in the axis of the cell and so close to the nucleus that the small clear space about the centrosome is tangent to the nuclear membrane. Four distinct radiations extend nearly or quite to the periphery of the cell. They appear finely granular. The presence upon the radiations of conspicuous granules surrounded by small clear spaces can be seen. The two radiations nearest the axis of the cell appear connected by a cross fibre, which extends between two of the larger granules mentioned.

In Figure 11 there is a distinct centred system with its centrosome in the axis of the cell and near the nucleus. About the centrosome is an imperfectly described circle of granules, four of which lie on the paths of radiations from the centre. In this respect, the system is one of the "second type" (page 114), but the region bounded by the circle of granules is rather lighter than the surrounding cytoplasm, instead of denser, as in Figure 3. A small neuroglia nucleus lies close upon one side of the cell.

Figure 12 shows a clear circle tangent to the nucleus and in the cell axis. At the centre of the clear circle are three indistinctly defined granules, from which several faint radiations extend into the cytoplasm.

Figure 13 exhibits a remarkable complexity of the centred system. The cytoplasm in this case was practically unstained, yet its fibres stood out with much clearness. This cell shows to advantage the presence of secondary centres. The primary centre, or centrosome, is easily distinguished as lying in the cell axis and in being the point from which proceed several radiations which extend in straight lines almost to the periphery of the cell. Upon these radiations are conspicuous granules from which extend secondary radiations. The secondary radiations sometimes appear to connect certain larger granules on two different primary radiations. This cell is one of the first type, lacking anything that could be called a "sphere."

V. General Conclusions.

1. MITOSIS IN THE NERVOUS FUNDAMENTS.

To summarize briefly the process of mitosis as seen in the cells of the ganglionic fundaments:

The prophase is accompanied by a turgescence of the cell; a distinct cell membrane is formed; the nuclear membrane disappears; the chromatin takes the form of nearly spherical chromosomes; the region between the chromosomes and the cell membrane is nearly or quite clear; a spindle appears with its centrosomes very minute, if visible at all.

In the metaphase a distinct cell membrane is still present; the spindle with its equatorial plate of chromosomes lies sharply outlined in the cell body, which is otherwise nearly or quite free from any solid material; generally the centrosomes are clearly to be seen at the spindle poles and often they become fairly conspicuous objects.

In the later phases the chromosomes separate and move toward the poles, each daughter group fusing into a compact mass, which is concave on its polar side; the centrosome remains visible at the apex of the old spindle, the end of which forms a lightly staining region between the centrosome and the concave surface of the chromatic mass; the interzonal filaments occupy a barrel-shaped region; an equatorial constriction of the cell membrane appears. The ingrowth or differentiation of an equatorial membrane between the two daughter cells follows, accompanied by the constriction of the barrel-shaped figure to the form of two cones with apices together at the plane of the equatorial membrane. As a result of this decrease in the volume of the figure, some of the substance of the barrel-shaped figure, including a few of its filaments, is left outside the limits of the constricted figure. This substance disappears later.

During the forming of the equatorial membrane, the old cell membrane (now become the daughter-cell membranes) undergoes degeneration, and finally the new equatorial membrane also disappears. At this period, then, the constricted figure lies sharply outlined in an irregular clear space which is not definitely outlined, not enclosed in a membrane, and not divided by an equatorial membrane (Fig. 30). The interzonal filaments degenerate, leaving the two daughter chromatic masses and their accompanying polar structures lying in a common clear space (Fig. 33, α and β). The chromatic mass is the nucleus; the lightly stained conical polar region with the centrosome at its apex is the fundament of the cytoplasm.

The chromatic mass, enclosed within its new nuclear membrane, breaks up into granules, which become the chromatic parts of the resting nuclear network. The polar concavity persists during the earlier growth of the nucleus.

The polar cytoplasmic fundament increases in volume along with the nucleus, the centrosome persisting through all the growth of the cytoplasm, and becoming the centre of the radiating system of the resting cell.

That the spherical membrane seen in the prophase (Fig. 21) is a cell membrane and not an expanded nuclear membrane admits of no doubt when its fate is considered. It is identical with the membrane which encloses the clear space surrounding the figure in the metaphase (Figs. 22–24), and it is this membrane which constricts during the later phases, in connection with the formation of the equatorial membrane. Moreover, the centrosome in the daughter cell lies outside the nucleus. During the prophase, therefore, we should not expect to find it within the nuclear membrane.

The peculiar feature in the reconstitution of the daughter cells is the complete degeneration, during the telophase, of all parts of the mother cell outside the limits of the spindle figure, together with the newly formed equatorial membrane. Still later, the interzonal filaments having disappeared, there comes a period when all the living parts of each daughter cell consist of the compact chromatic mass (nucleus) and its polar region (cytoplasmic fundament), including the centrosome.

2. Development of the Nerve Cells.

In the progress of the nucleus toward the resting condition there is little, if any, increase in the volume of the chromatin. The growth of the nucleus is due to the increase in its fluid contents. As nearly as can be judged, the total volume of the scant chromatin in the large resting nucleus is about the same as the volume of the compact chromatic mass immediately after mitosis.

The growth of the cytoplasmic fundament involves the assimilation of outside material and its transformation into a dense protoplasm. As already stated, the cytoplasm in the smaller cells is denser, more finely granular and homogeneous than in the larger cells. It seems highly probable that the fluid material resulting from the degeneration of parts of the mother cell is utilized by the growing cytoplasm of the daughter cells, which finally come to occupy the territory originally filled by the mother cell. It is commonly the case that the cytoplasm becomes more or less fluid during the earlier phases of mitosis, having a clear appearance in preparations; especially is this the case immediately about the nucleus or the spindle. But in the usual forms of mitosis, the cytoplasmic structure reappears throughout the body of each daughter cell during the later phases, and the daughter nucleus, during its reconstitution, lies in a cytoplasmic mass which is obviously half that of the mother cell. The mother cytoplasm undergoes only a temporary alteration in structure. In the mitosis of the cells of the ganglionic fundaments with which we are dealing, there is, on the contrary, nothing which suggests the reappearance of the old cytoplasmic structure throughout the bodies of the daughter cells, but a growth of new cytoplasm takes place progressively outward from the polar region of the nucleus. *The end of the old spindle lying between the centrosome and the daughter chromatic mass (nucleus), together with the centrosome, contains the substance which effects the regeneration of the cytoplasm.*

This regeneration of the cytoplasm of newly divided cells takes place only among the cells of the nervous fundaments. It is found in none of the other regenerating tissues. In all of the preparations from which my figures have been taken, mitosis of the ordinary type may be found in other regenerating tissues. In the dividing cells of the cicatrix there is at all phases a more or less dense mass of cytoplasm about the spindle figure. The mother cytoplasm in these cases is divided in the usual way, one half persisting, without degeneration, about each daughter nucleus. In cells of the epidermis, of the alimentary epithelium, and in nuclei lying in the muscle layers, the mitosis is accompanied by no sign of degeneration and subsequent regeneration of the cytoplasm. In cells of the brain sheath itself, or in cells lying immediately outside it, the telophase shows some dense cytoplasm about each daughter nucleus, whereas, in the same preparations, telophases within the brain fundament exhibit the conditions which have been described, — the absence of structure outside the spindle figure itself. Moreover, in the nervous fundaments, at least in their later stages, all of the mitoses are of the type described. No dividing cells whatever were found presenting conditions other than these. At what period of regeneration mitosis of this type appears, I am unable to say. My preparations have not as yet yielded stages favorable for determining conditions in the very earliest fundaments. In some preparations otherwise favorable, mitosis in the fundaments is rare or absent, indicating that the animal was killed during an interval between periods of cell increase. All of the mitoses described are from preparations in which the fundaments are well established, containing, in their deeper parts, cells which have ceased dividing and assumed the appearance characteristic of nerve cells.

It is not certain that all the products of division, in fundaments at this stage, immediately acquire a large cytoplasmic mass and become differentiated into nerve cells. It is evident that, at some earlier period of the fundament, this could not possibly be so, else the supply of undifferentiated cells would be exhausted before the needful number of nerve cells had been produced. It must be that up to a certain period one or both of two sister nuclei acquire only scant cytoplasm after a division, retaining their embryonic character for the purpose of further division. After a sufficient number of nuclei have been produced, it may be that both of two sister nuclei give rise to nerve cells, while some of the embryonic cells cease dividing without undergoing differentiation into nerve cells, remaining as the small embryonic cells seen about the posterior border of the full-grown brain. Or it may be that one of two sister nuclei gives rise to a nerve cell, the other ceasing to divide and remaining as an undifferentiated cell.

Little can be said as to the origin of the neuroglia of the regenerated brain and cord. As the new nerve cells become differentiated, there also appear among them small nuclei similar in character to nuclei — doubtless of non-nervous nature — found in the normal brain and cord. It is not improbable that cells of the early fundaments give rise to the neuroglia as well as to the nervous nuclei, — a differentiation from the indifferent cicatricial cells in two directions. It is also possible, however, that the neuroglia may be derived from cells having a common origin with those that give rise to the sheath.

3. Persistence of the Centrosome.

A definite centrosome is first to be seen at the time of the formation of the spindle in the prophase. It is an extremely minute body at that time, but during the later phases it increases in size, appearing as a single, very dark, spherical granule lying at the pole of the spindle. At the close of mitosis it increases considerably in size, and sometimes appears less intensely stained. In Figures 31–35 (Plate **5**) the centrosome is seen to be much larger than at any stage of the mitotic figure. In Figure 34 it is not a spherical granule, but is somewhat elongated. In cells showing a greater development of the cytoplasm (Figures 36–38) there is generally present a large dark granule near the centre of the cytoplasmic mass. In as early conditions as those seen in Figures 32 *b*, 35, 37, and 38, the differentiation of a clear space, or a darker circle, about the centrosome, or some evidence of radiations can sometimes be seen. The centrosome is largest immediately after mitosis. As the cytoplasm increases in volume the centrosome becomes somewhat smaller. In cells like those of Figure 39, where the nucleus is in typical resting condition, the small cytoplasmic mass contains the centrosome, frequently with evidences of concentric and radiating structures about it. With further increase in the size of the cell and the volume of the cytoplasm (Figures 40–42) there is to be seen a centred system — centrosome, clear space and radiations — comparable in all respects to the system seen in the mature nerve cell.

In all stages of development between the last mitosis and the mature cell, the centrosome and its accompanying structures are so frequently met with that one is warranted in concluding that they are generally present.

It is evident, then, that the centrosome of mitosis is present during the earliest stages in the reconstitution of the daughter cells, that it persists during the growth of the cell, becoming associated with certain concentric structures and radiations, and becomes finally the central body of the complex system of radiating and intersecting fibres found in the fully differentiated nerve cell. This is true for the regenerated cells. That it will be found true in the case of nerve cells developed by the normal embryonic process is hardly to be doubted.

4. The Centrosome in Nerve Cells.

In transverse sections of a ganglion the cells are most likely to lie with their axes nearly parallel to the plane of cutting. In such sections evidences of the centred system are often to be found in the majority of the pear-shaped nerve cells. Thus the three cells of Figures 9–11 (Plate **2**), from a regenerated brain, lay side by side in the same section.

A centred system is not to be made out, however, in every cell of a section. Even if the structure is one generally present, we should not expect to be able to see it in all cells, for only the most favorable conditions could bring it to view. If the axis of the cell is not approximately parallel to the plane of cutting, the cell is likely to be cut so that the centrosome is not in the same section with the nucleus, — a condition which increases the difficulty of identification. So delicate a structure may often be obscured by some of the darkly staining masses of the cytoplasm. Considering the difficulties of observation, then, the centred system can be made out in so large a proportion of cells as to justify the belief that it is a structure usually, if not always, present in the mature nerve cells.

The largest cells of the brain and subœsophageal ganglion were least satisfactory for showing the presence of this structure. It was found with greatest frequency in cells of medium size, like those shown in Figures 1–4.

The "centrosomes" and "spheres" described for nerve cells by various authors present such widely different conditions as to suggest that they are not all homologous structures. For example, the condition in the centred system as I have found it in the earthworm is in no way similar to the sharply outlined homogeneous sphere and its numerous central granules described by von Lenhossék for spinal ganglion cells of the frog. The structure in such a cell as is represented in my Figure 3 may suggest his "sphere," yet it differs in being bounded by a layer of granules which occur on the radial fibres. Von Lenhossék found no granules bounding his sphere, nor any radiations.

The structure described by Dehler resembles that of von Lenhossék, being equally unlike anything found in the earthworm.

It is not impossible that the centrosome of mitosis, persisting in the resting cell, may give rise to structures differing as widely as the centrosome and sphere of von Lenhossék and Dehler differ from the centred system which I have described. A fuller knowledge of the structures described by them is needful. As long as they can be interpreted as sections of a "spiral figure' (Holmgren), or as wandering nucleoli (Rohde), a detailed comparison of these with the centred system is hardly warranted.

The methods used by Schaffer were not specially adapted to the study of finer cytoplasmic structure. McClure examined Lumbricus and found no evidence of the centrosome. The centrosome and sphere described by him for the nerve cells of other invertebrates exhibited no radial structure comparable to the radiating system I have described. Hunter sometimes found in ascidians "well developed astral rays" proceeding from the central homogeneous sphere with its centrosomes. Such a cell as that shown in my Figure 3 presents somewhat similar conditions.

Miss Lewis found in Clymene producta a centred system, — central granules and fine radiations, — with the additional complication of a sphere having a diameter perhaps one-third that of the cell. The condensed central region of the cell in my Figure 4 resembles such a sphere.

The structures most nearly resembling the centred system seen in the earthworm are those described by Bühler ('95) for brain cells of the lizard and ('98) for nerve cells of amphibians and mammals. In the later paper Bühler finds in some cells a centred system with its one or two central granules lying close to the nucleus and fine radiations extending toward the cell periphery, and in the same cell he also finds a concentric arrangement about the centre of the cytoplasmic mass, strongly suggesting the sphere of von Lenhossék. In other cells he finds a "spiral figure" similar to that described by Holmgren. These conditions suggest that the spheres of von Lenhossék and Dehler may be structures in no way connected with a centred system of fibrils, and that both structures may be present in the same cells.

The theory of the structure of the centred system, as proposed by Bühler, is strongly supported by my results. Bühler believes that the centrosome is the insertion point of the stronger fibrils, which may extend to the periphery of the cell. Other fibrils may not insert in the centrosome, but in the granules of the microsome stratum which constitutes the boundary of the sphere, or in large granules borne upon the primary radiations. The cell granules are, in general, the insertion points of fibrils, and the granules are larger, the stronger and more numerous the fibrils that insert in them. Accordingly, the centre of the entire system — the centrosome — is the most conspicuous granule. The system of primary, secondary, and tertiary fibrils which I have described presents exactly these conditions. The fibrils lose in prominence the farther removed they are from the centre. Therefore the primary radiations are oftenest seen. The granules that give rise to secondary radiations may be called secondary centrosomes. We may thus have centrosomes of lower and lower degrees of importance until the limit is reached, — the ordinary microsome.

Reinke ('94) finds secondary and tertiary centrosomes. He advances the proposition that a centrosome is potentially present in any microsome of the cell, and that it is not an organ *sui generis*, like the nucleus. Centrosomes and microsomes, he believes, are mechanical centres. A centrosome may arise at any point when needed, by the aggregation of microsomes. Similar views were expressed by Watasé ('93). Mead ('98) shows that in the maturation of the egg of Chætopterus a large number of asters arise in the cytoplasm. They are finally reduced to two, which become the asters of the maturation spindle.

The presence of the secondary and tertiary centres in the nerve cell is not inconsistent with the belief that the primary centrosome is the centrosome left from the last mitosis. The continuity of the centrosome of mitosis with that of the resting cells has been established in many cells other than nerve cells. That a centrosome may in some cases arise *de novo* must be granted in view of the results obtained by Mead in Chætopterus. Where the centrosome is continuous it may be regarded as a permanently differentiated microsome of special functional importance. After a mitosis it persists in the resting cell and marks the starting-point of the centred system of the mature cell. As the cytoplasm of the growing cell increases, the primary centrosome becomes connected, by means of fibrils, with other granules of the new cytoplasm. With continued growth of the cytoplasm, the radiating network develops from the centre outwards, being composed of "centrosomes" and radiating fibrils of lower and lower degrees of importance according to their distance from the primary centre. This is substantially the centred system described by Heidenhain.

That the function of such a system is a mechanical one appears most probable. The centrosome is generally believed to possess an important rôle in connection with the motor activities of cells, whether of the cell as a whole (leucocytes), or of appendages of the cell (cilia; flagellum of the spermatozoön), or in the movements observed in mitosis. In the absence of known motor activities in mature nerve cells, the most likely function for the centred system is that of mechanical support.

I have found no evidence whatever that the primary centrosome of the nerve cell ever resumes its mitotic functions. In all of the regenerating worms examined, no typical nerve cells with processes were found showing any change that would suggest the possibility of their dividing.

As already mentioned (pp. 78–80), masses of dividing cells are found occasionally in the old ganglia of a regenerating worm, but no such cell proliferation is to be found in the cord of a normal worm. These cell masses probably arise from "indifferent" cells which, in the early history of the cord, ceased dividing and failed to develop into nerve cells, retaining their embryonic character. Small cells, apparently without processes and having nuclei similar to those of the nerve cells, are to be found in the normal brain and cord. The injury to the nervous system is a stimulus which may set some of these cells to dividing. The purpose of cell increase in ganglia many segments back of the region of injury is not apparent. The stimulus of the injury is not restricted to the injured segment, and, in response to it, cell proliferation may occur where it is of no direct advantage in the regeneration of the new nervous parts.

In conclusion, it is to be observed that the centrosome and the nerve process in the earthworm occupy a definite position in relation to each other and the nucleus. They are always on opposite sides of the nucleus, the centrosome occupying the greater cytoplasmic mass. The point of origin of the process may therefore be considered to be determined at as early a period as the telophase of the last mitosis in the history of the cell. The chromatic mass is the nucleus. The polar region of the spindle occupies the position of the cytoplasmic fundament. The nerve process will be developed from the equatorial side of the nucleus. In the smallest cells that give evidence of any nerve process, the centrosome and process are on opposite sides of the nucleus.

VI. The Centrosome in Cells of the Epidermis.

A study of the cells of both the old and the regenerated epidermis brings to light strong evidence for the presence of the centrosome in the resting cell of this derivative of the ectoderm. The cells of the old epidermis are less favorable for the detection of the centrosome than the regenerated cells. The old epidermis consists of much elongated columnar cells, whose contents are often coarsely granular. The cells of a recently formed epidermis are more flattened and their contents finely granular.

In Figure 43 (Plate 6) are shown two cells from the epidermis of the anterior end of a normal worm. In both of these there is a conspicuous deeply stained spherical granule, lying in a clear space directly at the deeper end of the much elongated nucleus. In the cell at the left in the figure this granule (*c'so.*) is the only prominent object in the cytoplasm. In the cell at the right, at the outer end of the nucleus, is a region in which are scattered a dozen or more deeply stained granules.

Two of them lying very close together occupy a slightly clearer space just at the outer end of the nucleus. The condition in the right cell, taken by itself, makes doubtful the interpretation of any of its granules as a centrosome. The large granule at the deeper end of the nucleus, or the pair in the small clear space at its outer end, or both, might pass for centrosomes. Or they might almost equally well be considered accidental granules of the kind which forms the group at the outer end of the nucleus. It must be noted, however, that the granule at the inner end is in some respects unique. It is larger than any of the others, its clear space is better defined, and the end of the nucleus is sharply invaginated at the region nearest the granule, the curvature of the invagination corresponding to the outline of the clear space. These facts, together with the fact that the next cell contains a similar granule, similarly located, and without the presence in the cell of any other like bodies, make it highly probable that the granule at the inner end of the nucleus of each cell is not an accidental thing.

These two cells well represent the conditions in the old epidermis. Very many, perhaps most, of the cells resemble the cell at the right in Figure 43. There are several, or very many, large granules in the cytoplasm, often at both ends of the nucleus. Frequently one of these granules lying near the inner end of the nucleus will appear slightly larger than the others, or it may lie in a clear space; yet it is not sufficiently peculiar to justify considering it anything but an accidental granule like others in the cytoplasm. The combined evidence from all such cells affords alone no conclusive argument for the presence of a centrosome. But very often there are found cells like the left one of the two in Figure 43, where there is a single conspicuous granule, which is generally situated not far from the inner end of the nucleus. In rare cases some weak radiations can be detected. It is not uncommon to find the nucleus invaginated at its inner end, as in the right cell. These granules are doubtless "centrosomes" in the sense that such bodies in resting cells are so called, without knowledge as to their history or function. The occurrence of cells with the single definitely located granule makes it likely that in cells whose cytoplasm is filled with large granules the centrosome is present, but its identity is rendered doubtful by the presence of other bodies of similar appearance.

Figures 44 and 45 represent cells from recently regenerated epidermis. A thin layer of cuticula is present. The nuclei are more nearly spherical than in the old epidermis, and the cells are more flattened. Often no distinct cell limits can be seen. These figures are from sublimate preparations stained in Kernschwartz and safranin. In Figure 44 the middle nucleus has an irregular outline on the side toward the greater cytoplasmic mass. Two small granules lie close to the nuclear membrane, each one opposite a slight concavity of the nucleus. Each granule is surrounded by a clear space. From both granules radiations extend into the cytoplasm, some of them going in straight lines nearly to the cell periphery, others (those directly opposite the nucleus, in the middle region of the cell) showing an arrangement like that described in the nerve cells. The primary radiations from the centre meet granules from which go off secondary radiations, resulting in something of a radiating network of fibres with granules at their intersections. The radiations, like those of the nerve cell, appear either as hyaline fibrils, or as rows of granules. The presence of the two central granules in Figure 44 suggests preparation for mitosis.

In Figure 45 the larger nucleus has a sharp invagination at its deeper end. Opposite the invagination is a granule with a complex radiating system about it. Primary, secondary, and tertiary radiations may be detected.

VII. Mitosis in the Regenerating Epidermis.

Figures 46–52 (Plate 7) represent stages in the mitosis of cells in the regenerating epidermis of a single worm. Figure 46 shows a cell in the prophase. The chromatin has assumed the form of nearly spherical chromosomes. The nuclear membrane is still present, but indistinct or absent at the regions where the spindle comes into relation with the chromosomes. No distinct granules could be detected at the spindle poles. Well defined polar radiations are present. The cytoplasm is fairly dense throughout the cell, and there is a distinct cell membrane. The deformation of adjoining cells shows that the cell has increased in volume. This condition is followed by the total disappearance of the nuclear membrane, and the chromosomes are assembled into an equatorial plate. Figure 47 shows the daughter chromosomes on their way toward the poles. Indistinct interzonal filaments are present. The centrosomes are extremely minute, but definite granules. Numerous polar radiations extend to the periphery throughout the entire cell.

Figure 48 shows a cell seen from the surface of the epidermis, the axis of the nucleus being perpendicular to that of the cell. The nuclear figure is in the telophase with barrel-shaped interzonal region. The centrosomes could not be found. Figures 46–52 are, with the exception of Figure 48, all from a limited region of epidermis at the ventral edge of the cut end of the worm. Figure 48 is from a mass of cells more dorsally placed, and so near the end of the alimentary tract that its epidermal origin is perhaps doubtful. No other cells in this phase could be found in the preparation.

Figures 49–51 show late telophases in the same group of cells from which Figures 46 and 47 are taken. All of these cells show a peculiar condition of the cell membrane. In Figure 49 the interzonal filaments are constricted at the equator, and there is a distinct "Zwischenkörper." An equatorial membrane has formed between the daughter cells. The triangular clearer region on the deep side of the two cells can best be interpreted as the space from which the mother-cell membrane has receded in its constricting. In the daughter cell at the right there is a narrow clearer space immediately about the interzonal filaments and the chromatic mass. On the deep side this space is so sharply outlined as to appear bounded by a membrane. In the cell at the left there is something which appears like a faint membrane (*mb.′*) lying just within the old cell membrane.

In Figure 50 there is a remarkable doubling of cell membranes, and in Figure 51 a well defined membrane (*mb.′*) in each daughter cell evidently corresponds to the membrane *mb.′* in Figure 50. Outside each of these membranes in Figure 51 is a region corresponding to the regions in Figure 50 enclosed by the membranes, *mb.* In Figure 51, however, these two regions are indefinitely outlined.

These conditions would force upon us the conclusion that a new cell membrane is formed within the old membrane of each daughter cell, and that the old membrane finally disappears. A search through the epidermis of this animal failed to reveal other stages which would throw any more light upon the question.

A centrosome may be seen in the concavity of the chromatic mass in the right daughter cell of Figure 50, and in the left daughter cell of Figure 51. In the latter figure a distinct nuclear membrane is formed about the chromatin. Figure 52 shows two sister cells from the same region. The section is somewhat oblique to the surface of the epidermis. The nuclei have increased in size, the concavity still persisting. In the cell at the right the concavity of the nucleus is filled by a dense, finely granular mass containing the centrosome with some faint radiations. The presence of the centrosome at so late a period in the history of the young cell is evidence that the central granule of the radiating system of the resting cells (Figs. 44 and 45) is a true centrosome, remaining from the last mitosis.

VIII. Mitosis in the Subepidermal Cells of the Old Epidermis.

Figures 53–56 (Plate **8**) represent subepidermal cells, or basal cells of the epidermis. These cells occur wedged in between the deep ends of the columnar epidermal cells. In one worm of seven days' regeneration, many dividing cells were found among the subepidermal cells in five or six segments back of the injured segment. However, no mitosis was found in the elongated columnar epidermal cells of the same animal.

Figure 53 represents a cell in which the division is complete. The new nuclear membranes have been formed. The nuclei are cup-shaped, and the greater mass of chromatin is collected on the concave side of the nucleus. At the concavity of the nucleus in the lower cell may be seen the conical spindle region with a minute centrosome at its apex. In the upper cell there is a slightly denser region immediately outside the concavity of the nucleus, and at the centre of this denser region is the centrosome. Several indistinct granules lie at the edge of the denser region. There are some weak radiations from both centrosomes. A dividing cell membrane is present. This membrane is represented as if the cell were seen as a transparent object. The lower of the lines, *mb'*., is the intersection of the membrane with the upper surface of the old cell membrane; the upper line, *mb'*., is its deeper intersection. On the dividing membrane and in the axis of the old spindle (whose former position is marked by a darker region extending between the two nuclei) is a small dark mass, perhaps a "Zwischenkörper."

Figure 54 shows two sister cells. In one the concavity of the deeply cup-shaped nucleus, as well as a considerable space immediately outside of it, is filled by a mass of dense cytoplasm. The centrosome, an intensely staining granule with weak radiations, lies just outside the concavity of the nucleus. The condition of the young nucleus is characteristic. The chromatin is massed in a nearly solid layer on the concave side of the nucleus, while more or less isolated masses of chromatin extend from this layer to the equatorial surface of the nucleus. The upper nucleus of Figure 54 is seen in the direction of its (spindle) axis. The mass of chromatin which lines the cavity is seen as a nearly complete circular band.

A young cell whose nucleus has increased in size and lost something of its concavity is shown in Figure 55. A finely granular region separated from the outer coarser cytoplasm by a narrow clear space, and containing at its centre a prominent centrosome with some radiations, is seen at the polar concavity of the nucleus. The sister cell was immediately adjoining, but its axis was in an unfavorable position.

Figure 56 represents a cell in which the resting condition has been regained. There is still a slight flattening of the nucleus on one side, — the remains of the polar concavity. The centrosome, imbedded in a mass of cytoplasm denser and more finely granular than that of the rest of the cell, lies on the flattened side of the nucleus and directly opposite the flattened region. The sister cell was identified in the next section. It showed similar conditions as to the nucleus, slightly concave on one side, and the presence of a denser mass of cytoplasm at this region of the nucleus, but no definite centrosome could be seen.

A study of the earliest stages of regeneration may reveal that the new epidermis over the cicatrix owes its origin to the subepidermal cells rather than to the columnar cells of the old epidermis. The occurrence of mitosis in the subepidermal cells many segments back of the one injured recalls the fact of groups of actively dividing cells in ganglia remote from the cut end of the worm. The subepidermal cells may act as "Ersatzzellen," receiving an impulse toward mitosis even in segments remote from the injury.

IX. Some Peculiar Mitoses.

I desire to call attention briefly to certain dividing cells in a worm of seven days' regeneration. Directly under the new epidermis was a small mass of cells with nuclei like those of the epidermis. Abundant mitoses were found among these cells. Figure 57 shows a group of the cells with a dividing cell in the metaphase. All stages of mitosis could be found, presenting a series of conditions exhibiting no unusual features. There were telophases with chromatin solidly massed at the poles and a barrel-shaped interzonal region, the whole figure being imbedded in a mass of dense cytoplasm. Later stages showed the formation of an equatorial membrane, the constricting of the interzonal filaments and some evidence of a Zwischenkörper. The old cell membrane and the equatorial membrane eventually disappear, but at all stages there is some dense cytoplasm collected about the daughter chromatic masses. The cytoplasm of the resting nuclei is indefinitely outlined; there are no cell membranes.

Among these cells a few cases were found which exhibit exceptional conditions. These are shown in Figures 58–60. Figure 58 is the only cell of its kind which could be found. To describe it in terms of normal mitosis, there are two chromatic masses with some interzonal filaments extending in straight lines between them. Enclosing these straight fibres is a sharply defined membrane (*mb. nl.*) slightly constricted near the equatorial region. This membrane is less distinct in the neighborhood of the chromatic masses. It could not be determined whether the membrane enclosed the chromatin, or not. Outside the membrane several fibres could be seen curving from pole to pole. Figure 59 is, beyond all doubt, a later stage of the condition seen in Figure 58. The cell outlines are sharply defined, and the equatorial membrane has formed, dividing the cytoplasm. The membrane (*mb. nl.*) must be identical with the one similarly designated in Figure 58. It can now be seen to enclose the chromatin. It is deeply constricted at the equator, and some indistinct fibres extend, within this membrane, between the chromatic masses. Figure 60 is readily seen to be a stage following that of Figure 59. The division of the cytoplasm is complete, a clear space intervening between the two daughter cells. The membrane, *mb. nl.*, is very sharply constricted, and the two cells are still united by it. The chromatin is in the form of large granules. Between the two chromatic masses extend some fibres which become thicker and darker as they approach the chromatic masses.

A careful search through the series failed to reveal any other stages in this process of division, and nothing like it was seen in other worms. It can hardly be doubted that the membrane, *mb. nl.*, of Figure 60 is a nuclear membrane. The membrane, *mb. nl.*, of Figure 58 is therefore a nuclear membrane. Is it the old nuclear membrane, or a new one? The question cannot be answered with the evidence at hand. Early stages of mitosis are present in abundance, but none showed any sign of the persistence of the old nuclear membrane. However, divisions of this type are so rare that we may readily suppose its earlier stages to be absent in the preparation. If *mb. nl.* is the old nuclear membrane, we have here a case of indirect cell-division, during which the nuclear membrane persists and divides by constriction in amitotic fashion. In some Protozoa the nuclear membrane normally persists during mitosis. It has been maintained by some writers that, in ordinary mitosis, the nuclear outline persists and can be made visible by certain methods (Pfitzner, '83, '86; Waldeyer, '88).

The other alternative is that *mb. nl.* is a *new* nuclear membrane, formed about both chromatic masses during the early telophase and secondarily dividing by constriction. Whatever the proper explanation, the condition is of sufficient interest to invite an effort toward obtaining additional stages in the process.

X. Summary.

I. There is commonly present in the nerve cells of Lumbricidæ a centred system, consisting of centrosome and radiations.

1. The single centrosome (or rarely two, or even three, small granules lying close together) is found in the axis of the cell, on the side of the nucleus opposite the nerve process, and therefore on the side of the greatest cytoplasmic mass. It is generally not far from the nucleus and approximately at the centre of the cell as a whole.

2. Radiations consisting of fibrils bearing minute granules extend from the centrosome toward the periphery of the cell. Calling these "primary radiations," there may also be distinguished secondary radiations, which arise from certain of the larger granules in the course of the primary radiations. In rarer cases tertiary radiations may be found arising from granules in the secondary radiations. The centred system is therefore a complex one, consisting of a chief centre or centrosome, and numerous inferior centres situated throughout the cytoplasm, all with their corresponding sets of radiations, the whole system forming a radiating network whose complexity increases toward the periphery of the cell.

3. In most cases, no structure which could be called a centrosphere is present. The centrosome, as well as each of the inferior centres, is generally surrounded by a small clear space.

Sometimes the centrosome is surrounded by a narrow region of denser cytoplasm, and the primary radiations, where they intersect the periphery of this region, bear conspicuous granules. In other cases the centrosome lies in a central mass of slightly denser, more finely granular cytoplasm, of perhaps one-half the diameter of the cell, but not bounded by a layer of granules.

II. A centred system like that found in nerve cells of normal worms is found in regenerated nerve cells. Its chief centre, or centrosome, is the centrosome of the last mitosis in the history of the cell.

1. If the anterior five or ten segments of a worm be removed, the regeneration of a brain and a certain length of ventral cord (not yet segmented) takes place in the course of five weeks.

2. The epidermis is the chief source of cells which give rise to the new nervous parts.

3. In the old cord no evidence of mitosis is found among the large pear-shaped cells with processes.

4. In some cases, masses of actively dividing cells are found in ganglia many segments back of the region of injury. These masses probably owe their origin to certain small indifferent cells which have retained their embryonic character since the development of the cord.

These cell masses can take no part in the regeneration of ganglia anterior to the region of injury, except when such a mass arises at the place of injury.

The stimulus due to the injury is not restricted to the segment injured, but may cause mitosis among cells of embryonic character in ganglia remote from the region of injury.

5. The regeneration of ganglia is preceded by a forward growth of fibres from the cut end of the old cord. Cells of epidermal origin accumulate ventrally and laterally about this new fibre tract to form the fundament of the new ganglia.

The fibre bundle divides to encircle the alimentary canal. At a region dorsal to the canal, it becomes associated with a mass of cells lying dorsally and posteriorly to the fibre mass, and, together with these, constitutes the brain fundament.

6. The deeper cells of the nervous fundaments are the first to become differentiated into nerve cells. The more superficial cells long retain their embryonic character, continuing to divide actively after the deeper cells have become typical pear-shaped ganglion cells.

7. About the posterior dorsal surface of the normal brain there are some cells with scant cytoplasm, and lacking nerve processes. These are doubtless cells which, in the development of the brain, stopped dividing without becoming differentiated into nerve cells, retaining their embryonic character, perhaps for purposes of regeneration in case of injury.

8. In mitosis among cells of the nervous fundaments of about five weeks' regeneration, the following peculiarities are to be observed: —

a. Throughout the process of mitosis the body of the cell outside the limits of the spindle figure is practically homogeneous and clear.

b. A well defined cell membrane, formed during the prophase, becomes constricted in the telophase, and an equatorial membrane is formed between the daughter cells. During the later phases the old cell membrane, as well as the newly formed equatorial membrane, degenerates and disappears, leaving the two daughter chromatic masses, connected by the equatorially constricted interzonal filaments, lying free in an indefinitely outlined clear space.

c. The daughter chromosomes, having completed their migration toward the poles, fuse to form solid chromatic masses, concave on their polar sides. *The chromatic mass represents the nucleus.*

d. In the concavity of each chromatic mass is a sharply outlined, lightly stained, conical region, — the region of the old spindle-end, — with the centrosome at its apex. *This conical polar region is the fundament of the cytoplasm of the young cell.*

e. The interzonal filaments disappear, leaving the two chromatic masses and their accompanying polar structures lying free in a common, irregularly defined, clear space formerly occupied by the mother cell. *All the living parts of each daughter cell are comprised within the chromatic mass and its polar region.*

f. The two young sister cells may become separated by the pushing in of adjacent tissue between them.

g. The transformation of the chromatic mass into a resting nucleus involves the swelling of the newly formed nuclear membrane, the increase in the volume of its contents probably being due to the absorption of fluid material. The solid mass of chromatin meanwhile gradually breaks up into small granules which, together with the achromatic substance, form the loose peripheral nuclear network of the resting nucleus. During this process a nucleolus appears.

h. Accompanying these changes in the nucleus, the polar cytoplasmic fundament increases in volume, remaining always sharply outlined in the surrounding clear space. For a considerable period the growing cytoplasm is massed upon the concave polar side of the nucleus. At length the nuclear concavity disappears and the increasing cytoplasm envelops the entire nucleus. By far the greater mass of cytoplasm, however, always remains on the polar side of the nucleus.

i. The size and form of the typical pear-shaped nerve cell are finally attained as a result of the continued swelling of the nucleus, the increase in volume of its large polar body of cytoplasm, and the development of a nerve process from the smaller mass of cytoplasm on the equatorial side of the nucleus.

j. Distinct centrosomes are to be seen at the poles of the mitotic figure at all stages.

After the disappearance of the interzonal filaments the centrosome is found at the apex of the polar cytoplasmic fundament, attaining its greatest size at this period.

During the early growth of the cytoplasm the centrosome persists, generally being found not far from the centre of the cytoplasmic mass. At an early period evidences of concentric and radiating structure about the centrosome are seen.

With continued increase of the cytoplasm, the centrosome assumes its characteristic position in the axis of the cell near the nucleus, and becomes associated with a system of radiating fibres whose complexity increases until the conditions found in the mature cell (I. 2) are attained.

III. 1. Some resting cells of recently regenerated epidermis possess a centrosome and system of radiations similar to those of the nerve cells.

2. In the mitosis of cells in the regenerating epidermis the centrosome persists in the cytoplasm after the nucleus has regained the resting condition.

3. In the much elongated columnar cells of the epidermis of the normal worm, there is strong evidence for the presence of a centrosome. In these very attenuated cells, however, no radiating system could be detected.

4. The final stages of mitosis in some cells of the regenerating epidermis exhibit peculiar conditions of the cell membranes, pointing toward the conclusion that, after the division of the cytoplasm, a new cell membrane forms within the old cell membrane of each daughter cell, the original cell membrane disappearing.

IV. 1. The stimulus due to the injury may cause abundant mitosis among the subepidermal cells or basal cells of the epidermis, several segments back of the injured segment.

2. The centrosome of mitosis in these subepidermal cells persists in the cytoplasm after the cell has returned to the resting condition.

V. In certain cicatricial cells, evidently of epidermal origin, a few mitoses were found where, in the telophases, both daughter chromatic masses were enclosed within a common membrane of doubtful origin (a distinct outer cell membrane being also present). This membrane finally constricts and divides equatorially, becoming, apparently, the nuclear membrane of the two daughter nuclei.

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EXPLANATION OF PLATES.

All the figures were drawn with the aid of the camera lucida. Unless otherwise stated, all preparations were fixed in Flemming's stronger chromic-osmic-acetic mixture.

Owing to defective printing, centrosomes and chromatic granules sometimes appear as rings, instead of solid bodies.

ABBREVIATIONS.

a.	Anterior.
can.ali.	Alimentary canal.
chr.	Chromatic mass (nucleus).
cic.	Cicatrix (cicatricular tissue).
cl. mit.	Mitotic cell.
cl. pr'f.	Mass of proliferating cells.
c'so.	Centrosome.
cta.	Cuticula.
d.	Dorsal.
ec'drm.	Old epidermis.
ec'drm'.	Regenerated epidermis.
gn.	Ganglion.
gn. nov.	Fundament of ganglia.
gn. su'œs.	Fundament of brain.
mb.	Mother-cell membrane.
mb'.	New cell membrane.
mb. nl.	Nuclear membrane.
mu. crc.	Old circular muscles.
mu. crc'.	Regenerated circular muscles.
mu. lg.	Old longitudinal muscles.
mu. lg'.	Regenerated longitudinal muscles.
reg. pol.	Polar region; cytoplasmic fundament.
stmd.	Stomodæum.
te.	Testis.
trt. fbr.	Regenerated fibre tract.
tu.	Sheath of nerve cord.
tu'.	Cut end of old sheath.
*	In Figures 14–16, the * marks the point where the old epidermis ends and the regenerated epidermis begins.

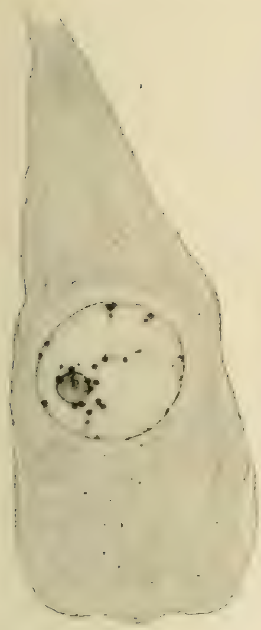
PLATE 1.

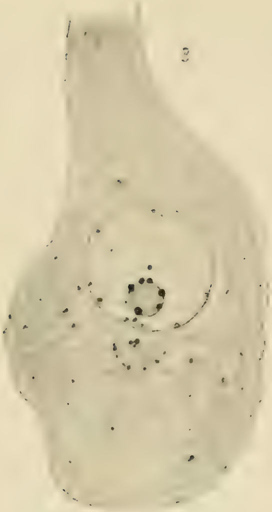
All the figures magnified 2000 diameters.

Figs. 1–3. Cells from the subœsophageal ganglion of a normal worm. Iron-hæmatoxylin.

Fig. 4. Cell from the brain of the same worm.

Figs. 5, 6. Cells from a posterior ganglion of a normal worm. Acetic-sublimate, iron-hæmatoxylin.





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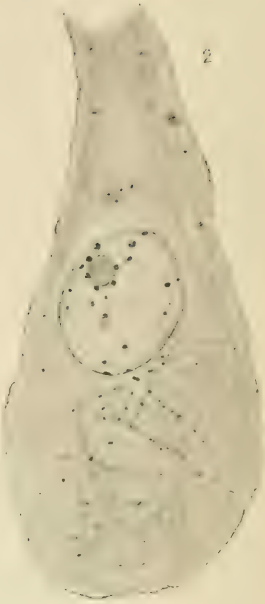

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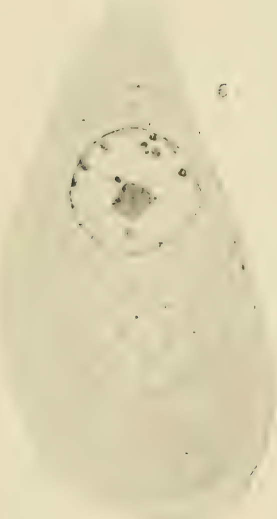

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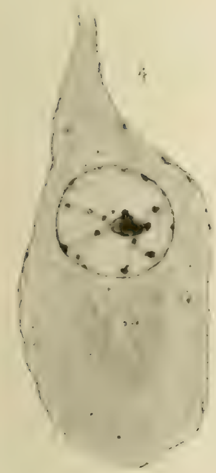

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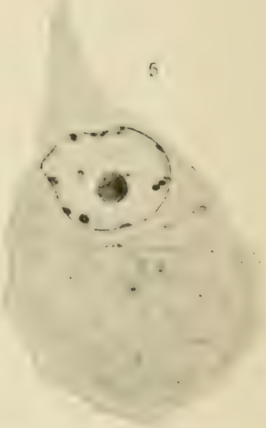

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PLATE 2.

All the figures magnified 2000 diameters.

Figs. 7–9. Smaller cells from the posterior dorsal region of the brain of a normal worm. Iron-hæmatoxylin.

Figs. 10–12. Cells from a regenerated brain after 34 days' regeneration. These three cells lay side by side in the same section. Iron-hæmatoxylin.

Fig. 13. Cell from a brain of 34 days' regeneration. Iron-hæmatoxylin.

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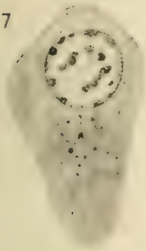

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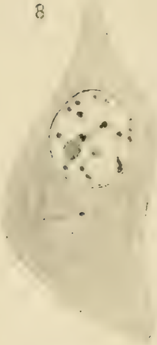

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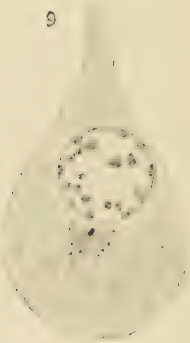

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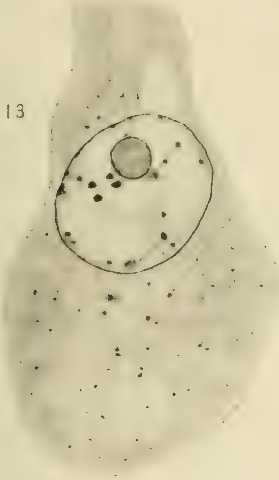

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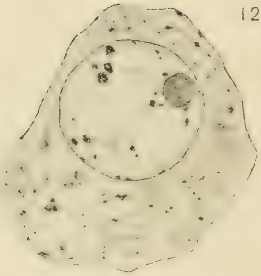

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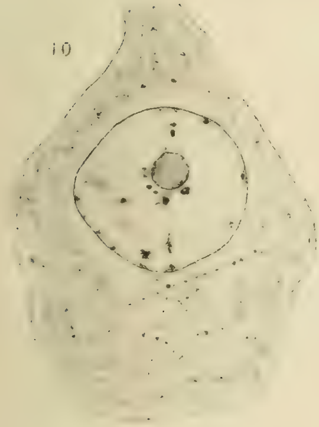

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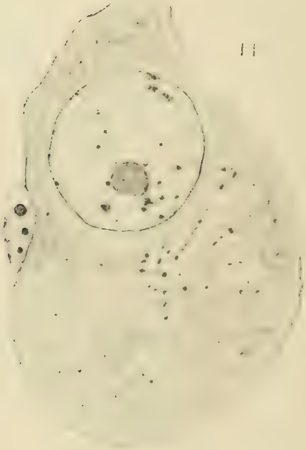


PLATE 3.

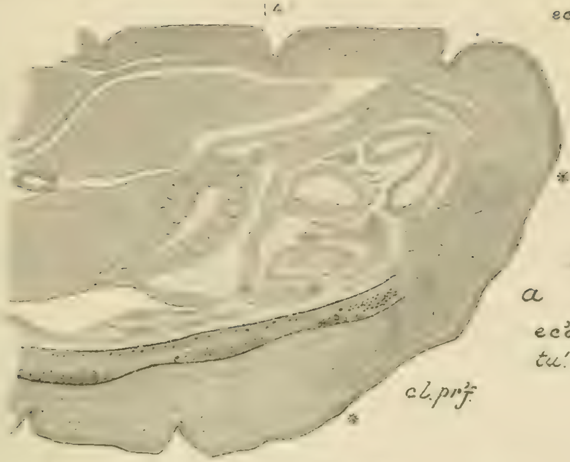
Fig. 14. Parasagittal section through the anterior end of a worm after 7 days' regeneration. × 25. Hermann's plat.-acet.-osm., iron-hæmatoxylin.

Fig. 15. Parasagittal section through the anterior end of a worm after 16 days' regeneration. × 25. Acetic-sublimate, iron-hæmatoxylin.

Fig 16. Parasagittal section through the anterior end of a worm after 24 days' regeneration. × 25. Acetic-sublimate, iron-hæmatoxylin.

Fig. 17. Spindle cells from the cicatrix of the worm from which Figure 14 is taken. (7 days' regeneration.) × 2000.

14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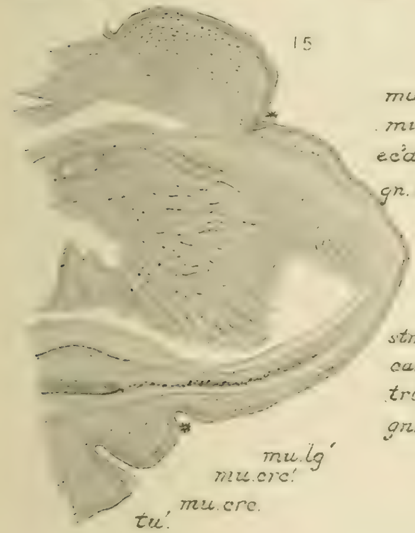
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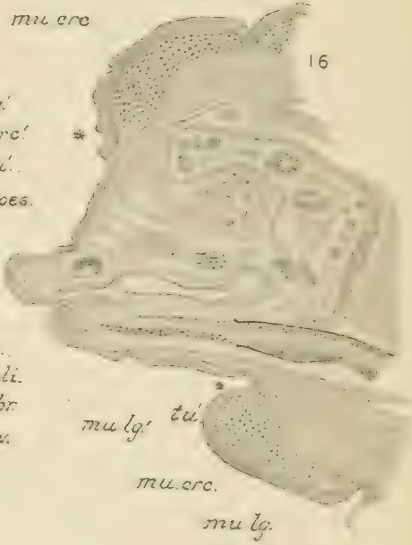
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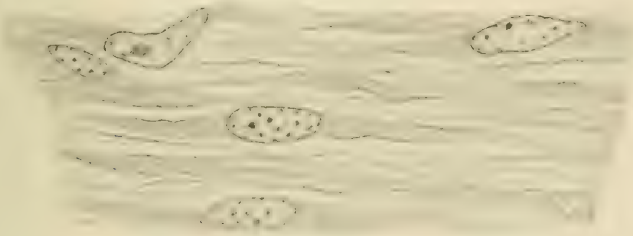

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PLATE 4.

Fig. 18. Anterior end of the nerve cord of Figure 14, showing a mass of newly formed cells. (7 days' regeneration.) × 160.

Fig. 19. Parasagittal section through the middle region of one lobe of the brain of a normal worm. × 160.

Fig. 20. Parasagittal section through the middle region of one lobe of a brain of 34 days' regeneration. × 160.

Fig. 21. A dividing cell in the prophase and one in the metaphase (one pole cut away) from a brain of 34 days' regeneration. × 2000. Iron-hæmatoxylin.

Fig. 22. Metaphase from a brain of 34 days' regeneration. × 2000. Iron-hæmatoxylin.

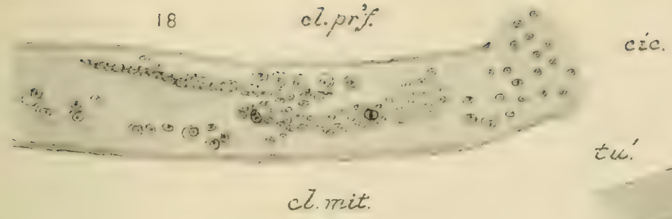
Fig. 23. Metaphase from the anterior end of a cord after 34 days' regeneration. × 2000. Gentian violet.

Fig. 24. Metaphase from a brain of 34 days' regeneration. × 2000. Gentian violet.

Fig. 25. Telophase from a brain of 34 days' regeneration. × 2000. Gentian violet.

Fig. 26. Telophase from the posterior dorsal region of a brain of 34 days' regeneration. × 2000. Iron-hæmatoxylin.

18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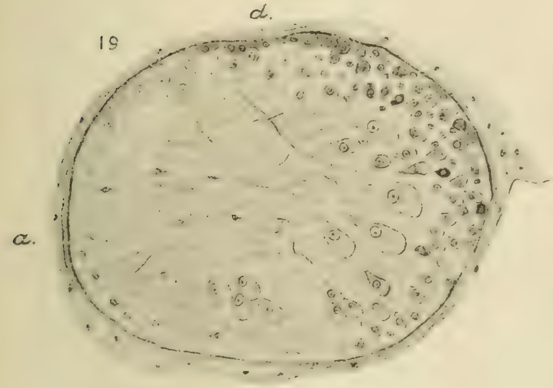

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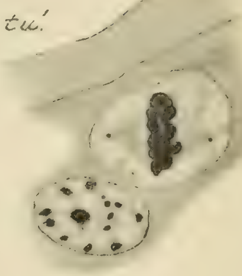

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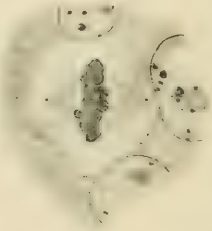

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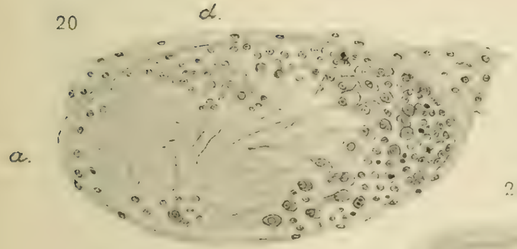

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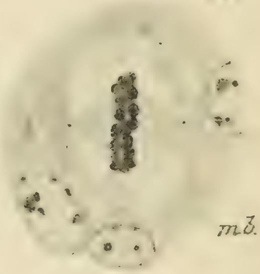

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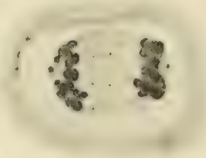

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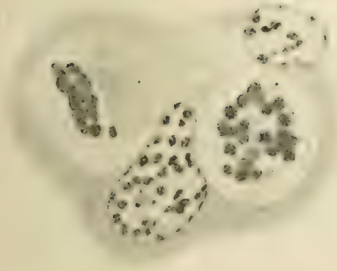

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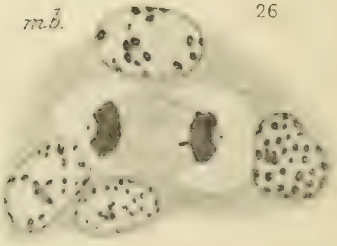

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PLATE 5.

All the figures magnified 2000 diameters.

Fig. 27. Telophase from a brain of 34 days' regeneration. Gentian violet.

Fig. 28. Telophase from a brain of 34 days' regeneration. One chromatic mass cut away. Gentian violet.

Fig. 29. Telophase from a brain of 34 days' regeneration. Reconstructed from two sections. Above it, a young cell. Iron-hæmatoxylin.

Fig. 30. Telophase from the anterior end of a cord after 34 days' regeneration. Gentian violet.

Fig. 31. Young cell (with several of the neighboring nuclei) from the posterior ventral region of a brain of 34 days' regeneration. Iron-hæmatoxylin.

Figs. 32*a*, 32*b*. A pair of young sister cells from a brain of 34 days' regeneration. The cells are in successive sections. Iron-hæmatoxylin.

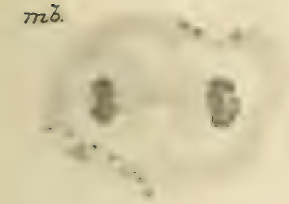
Fig. 33. Two pairs of young sister cells from a brain of 34 days' regeneration. α and β are one pair. The two cells of the other pair lie one over the other. γ is the upper of the two and the outline of the lower is indicated by δ. Gentian violet.

Figs. 34, 35. Young cells from the anterior end of a cord of 34 days' regeneration. Iron-hæmatoxylin.

Fig. 36. A group of cells from the posterior ventral region of a brain of 34 days' regeneration. At the centre of the group is a young cell. Iron-hæmatoxylin.

Fig. 37. Young cell from the dorsal region of a brain of 34 days' regeneration. Gentian violet.

27



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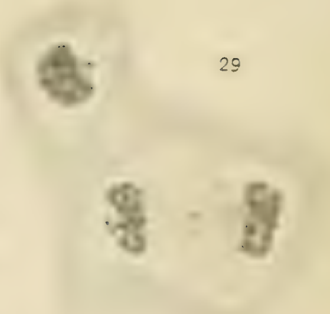

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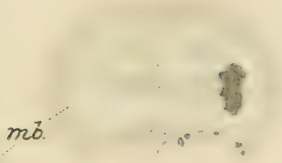

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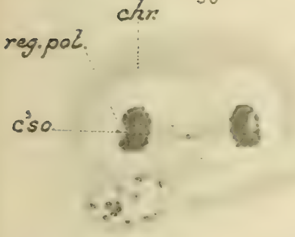
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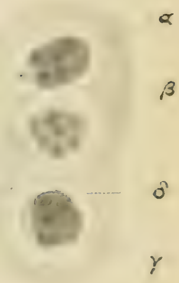

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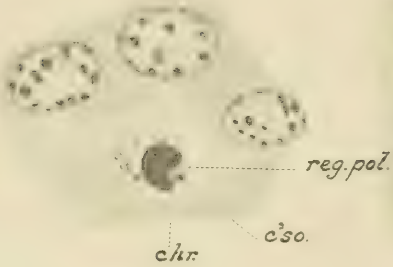
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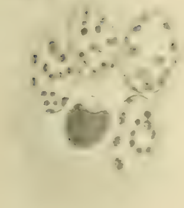
chr.

32 *a*



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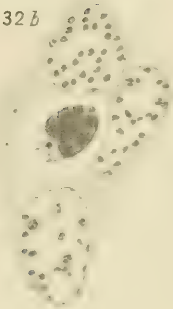

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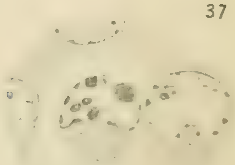

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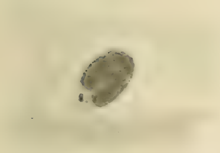

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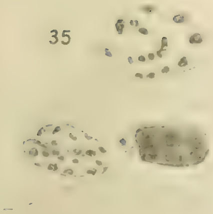

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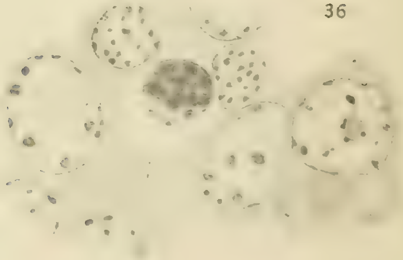


PLATE 6.

All the figures magnified 2000 diameters.

Fig. 38. Young cell (with several of the neighboring nuclei) from the anterior end of a cord of 34 days' regeneration. Iron-hæmatoxylin.

Fig. 39. Small cells with resting nuclei from the anterior end of a cord of 34 days' regeneration. Each of the two cells has a centrosome. Iron-hæmatoxylin.

Fig. 40. Cell with a greater mass of cytoplasm than in the cells of Figure 39; centrosome and radiations. From a brain of 34 days' regeneration. Iron-hæmatoxylin.

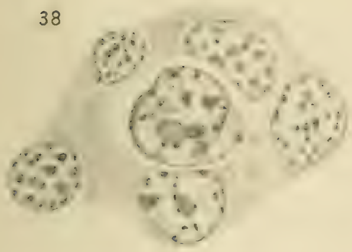
Fig. 41. Cell, similar to that of Figure 40, from a brain of 37 days' regeneration; centrosome and radiations. Iron-hæmatoxylin.

Fig. 42. Three cells from the anterior end of a cord of 34 days' regeneration. A centrosome with radiations may be seen near each of the two larger nuclei, on the side toward the greatest cytoplasmic mass. Iron-hæmatoxylin.

Fig. 43. Two cells from the epidermis of a normal worm. The centrosome is at the deeper end of each nucleus. Iron-hæmatoxylin.

Figs. 44, 45. Cells from regenerated epidermis, showing centrosomes and radiations. 16 days' regeneration. Acetic-sublimate, Kernschwartz and safranin.

38



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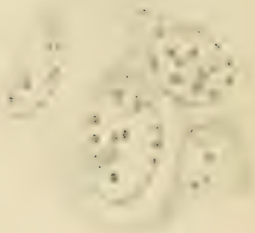

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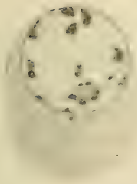

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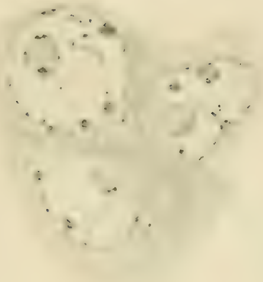

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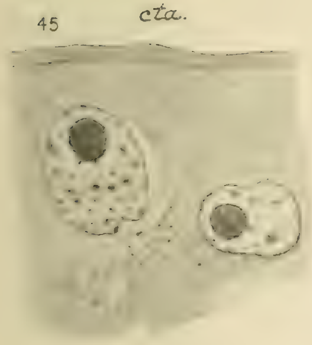

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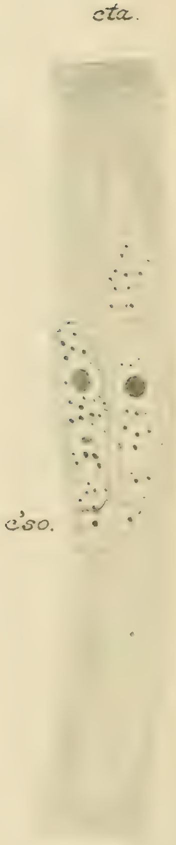

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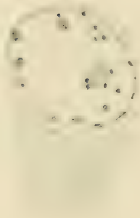

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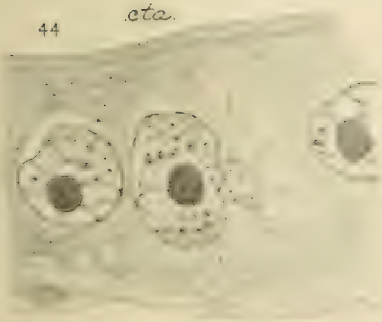
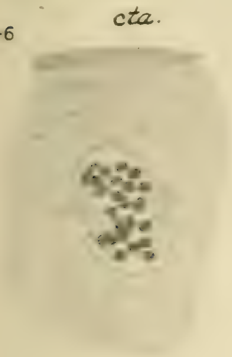


PLATE 7.

All the figures magnified 2000 diameters.

Figs. 46–52. Dividing or recently divided cells from the regenerated epidermis of a worm, after 11 days' regeneration. Hermann's plat.-acet.-osm., iron-hæmatoxylin. See pages 146–147 for a discussion of the membranes.

46



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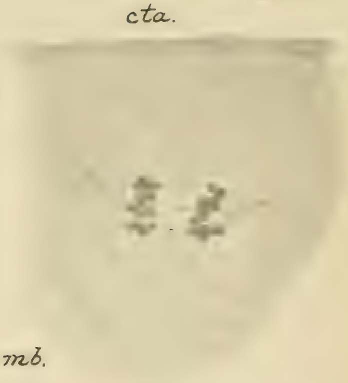

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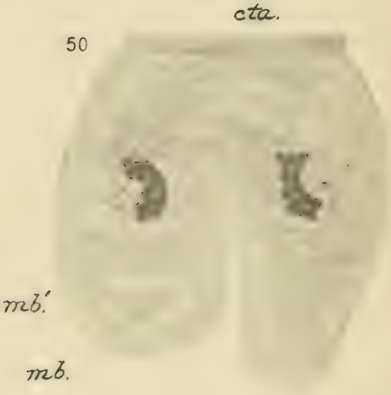

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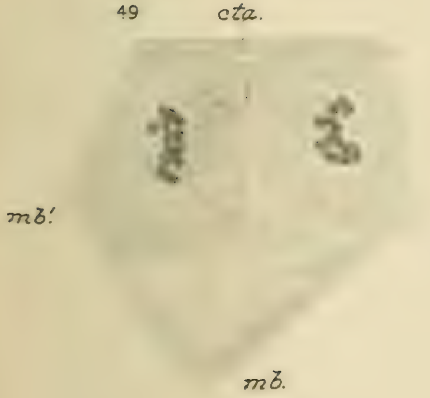

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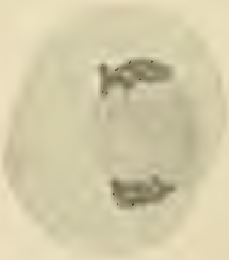

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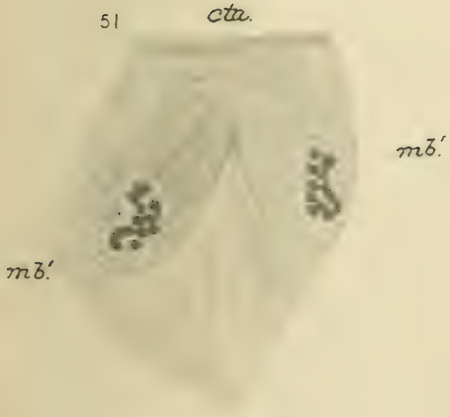

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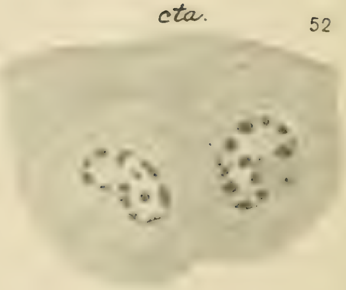

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